

EVOLUTIONARY TRENDS IN THE
CLASSIFICATION OF CAPITATE
HYDROIDS AND MEDUSAE



BY

WILLIAM J. REES, D.Sc.

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SYNOPSIS

The concept now outlined of evolutionary trends in Capitate hydroids departs considerably from the traditional ideas of evolution in gymnoblastic hydroids, and is based on a consideration of the species as a whole. The hydroids and their medusae are demonstrated to form mosaic patterns from which it is possible to create a single integrated classification to reflect relationships, and to replace the old dual system of unrelated separate systems.

No attempt has hitherto been made along these lines to consider the evolution of basic features and the relation of form to function in hydroids and their medusae. Here the significance of evolution in the hydranth, the development of a firm perisarc, the positioning of the gonophores and the gonophore itself are discussed in relation to the main trends in the group. The lower Corymorphines are demonstrated to be essentially primitive and from them are derived the Tubularoids, the *Acaulis-Myriothele* line and all the colonial Corynoidea.

In the outline classification which follows, four superfamilies are created, the Tubularoidea, the Tricelusoidea, the Acauloidea and the Corynoidea to denote well marked groups and evolutionary trends in the Capitata. Other changes include the recognition of the subfamilies Euphysinae, Boreohydrinae, Monocoryninae, Myriotheleinae and the creation of the Hydrocorynidae for *Hydrocoryne miurensis*.

1. INTRODUCTION

"It will assuredly seem strange that those principles of classification which have been acknowledged as the only sound ones, and which have been our guide in the study of every other group of the animal kingdom, should be almost entirely ignored in our attempts at a systematic arrangement of the Hydroids."

G. J. Allman, *Ann. Mag. Nat. Hist.* (3) vol. XIII, p. 345. 1864.

THE study of hydroids and their medusae gained great impetus about one hundred years ago with the classical researches of Michael Sars, Edward Forbes, Thomas Strehill Wright, Thomas Hincks, George James Allman and Philip Henry Gosse. These early field naturalists were fully aware of the need for extending the knowledge of the life history of these animals and considerable progress was made in linking up hydroids with their medusae, either by rearing young hydroids from medusae or in obtaining newly liberated medusae from hydroids. Even ninety years ago the dual system of classification—one for hydroids and the other for their planktonic medusae—was beginning to bedevil the classification of this group, and, although the relationship of a particular hydroid to a particular medusa might become known beyond doubt, the practice of using two entirely different names for different phases of the same species continued.

The opening words of Allman's pioneer efforts (1864) to achieve a sound basis for classification deplores this practice and goes on in another paragraph:

"Yet this is totally at variance with the first principles of natural classification and of a scientific nomenclature; and the sooner we get rid of it the better for the harmony of biological method, and the progress of that department of zoology in which it has prevailed."

It is obvious that Allman had a clearer grasp of first principles in the classification of hydroids and medusae than any of his contemporaries and his statement that "An adequate conception of the Hydroid can thus only be obtained by regarding it as the product of two factors, one of them finding its expression in the trophosome, and the other in the gonosome" was so far ahead of his time that even today we find few authors have caught up with this principle.¹

In capitate hydroids and medusae the need for maintaining a dual classification has almost disappeared although there are still gaps to be filled. A single classification for both hydroids and medusae of this group is now possible but to evolve a natural classification is much more difficult. The latter is basically an assessment of the true value of the various characters used in classification, that is, we must consider the mosaic to appreciate where a species stands in relation to others.

In recent years two papers have been written on interrelationships in gymnoblastic hydroids on the conventional lines of dealing with only one phase in the life history and without considering form in relation to function. Fraser's attempt (1943) need not be seriously considered (Text-fig. 1), but a very interesting paper on the origin of the hydroid family Corymorphidae appeared from the pen of P. L.

¹ We find that Fraser (1944) for instance, seldom gave any adequate description even of the newly-liberated medusae of the medusa-bearing species while some of his ideas on classification were almost pre-Hincks in concept.

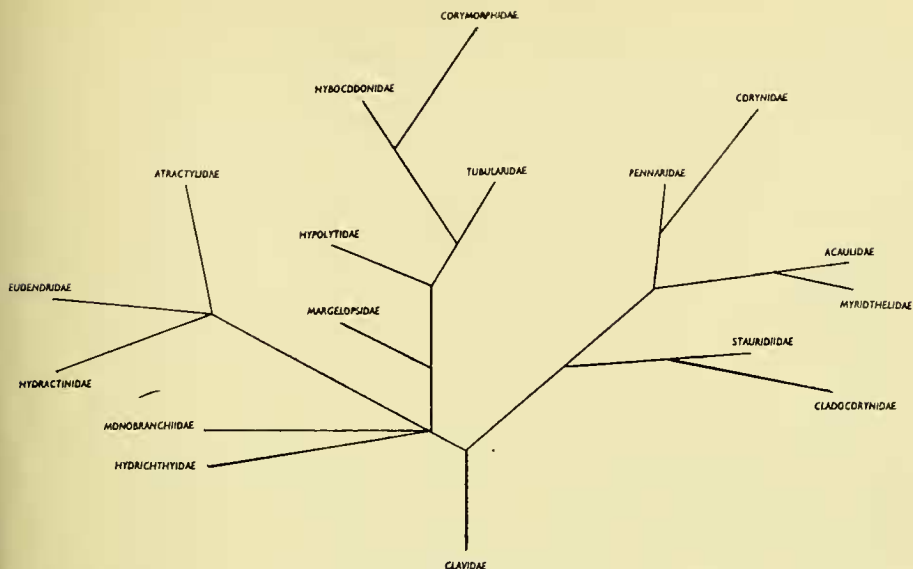


FIG. 1. Phylogeny in North American gymnoblastic hydroids as envisaged by Fraser (1943).

Kramp in 1949. In it he set forth his views on interrelationships in hydroids of the Corymorphidae, the Tubulariidae, Corynidae and related families. He followed Kühn (1913) in the view that the Corynidae are the most primitive (Text-fig. 2) and from which all other capitate forms are derived. He traced two separate lines of evolution called the *Tubularia*-line, and the *Corympha*-line, culminating in the Tubulariidae and Corymorphidae respectively.

This theory appeared plausible from the conventional approach, but years of experience on living hydroids and medusae at Plymouth and elsewhere had already inclined me to the belief that the less specialized Corymorphine hydroids were more primitive in all essentials than other capitate forms. The appearance of Dr. Kramp's paper renewed my interest in this question and although I could not accept the view that most of the solitary forms were derived from the colonial Corynidae, it was soon evident to me that any alternative theory on conventional lines would not solve the problem of relationship.

This led me to what I am inclined to call basic principles in the classification of hydroids and medusae in order to try to assess the evolutionary significance of the various features on which classifications are based. In attempting to establish basic principles from which to work, I am very conscious that some of them are possibly axiomatic in other fields of zoology and probably by no means new, but in the study of the Hydrozoa there has been remarkably little consideration given to fundamental questions of relating form to function and the probable evolution resulting from it.

In this paper it is not possible to present more than an outline of the Capitata

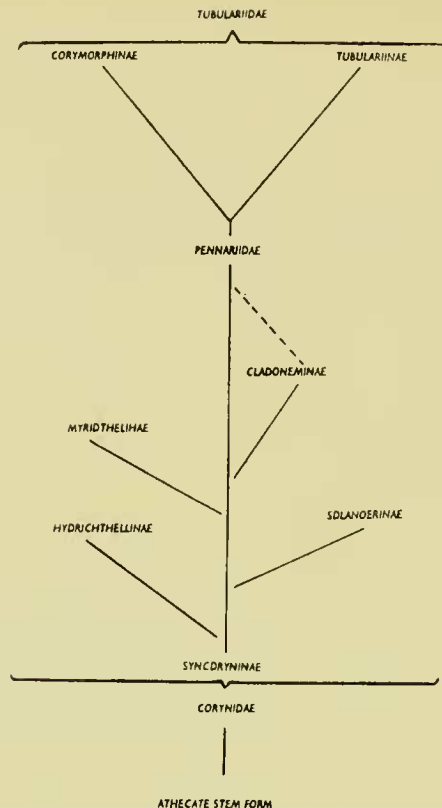


FIG. 2. Phylogeny in gymnoblastic hydroids according to Kühn (redrawn from Kühn, 1913).

and the way I think they have evolved, a concept which departs considerably from the traditional ideas of evolution in gymnoblastic hydroids. In order to make the paper intelligible to the general zoologist and the student, some of the facts have been repeated in the sections on mosaic patterns and relationships in order to clarify the general picture, and there are more illustrations than would be needed by the few specialists familiar with this group.

During the last twenty years I have gained much from earlier authors, and over such a period it is impossible now to be sure that I have acknowledged in the bibliography all whose ideas have influenced the development of this paper. It was not until 1950-51 that the ideas for its completion began to take shape, and although I explored other avenues, none, however, yielded so satisfactory an overall pattern of Capitate evolution as outlined here.

It is to the late Edward T. Browne that I owe the opportunity to begin the study

of this group at Plymouth from 1936 to 1940, the ultimate aim of which he envisaged as a single classification of hydroids and their medusae. I also wish to acknowledge with gratitude the encouragement I received from the late Edgar J. Allen, C.B.E., F.R.S., the late Stanley W. Kemp, F.R.S., and Dr. F. S. Russell, C.B.E., F.R.S., during the time I was a member of the scientific staff of the Plymouth Laboratory.

This paper could not have been written, however, without the many facilities granted to me at the British Museum (Natural History), and, in particular, I wish to thank Sir Gavin de Beer, F.R.S., for much encouragement. I am very grateful to Professor Hjalmar Broch for many stimulating discussions in Oslo, in September, 1955, but I do not wish to imply that he is in agreement with all or any part of this paper. I also wish to thank Dr. Marta Vannucci for reading the manuscript and for suggesting the inclusion of Figure 58 and my colleague Mr. Ernest White for much assistance in the preparation of the report. Other acknowledgments are given in the text.

2. EVOLUTION IN THE POLYP AND DIVISION OF LABOUR

(a) *Evolution in the polyp*

Sessile colonial invertebrates are generally considered to have arisen from free swimming solitary individuals which have adopted a sedentary habit and have

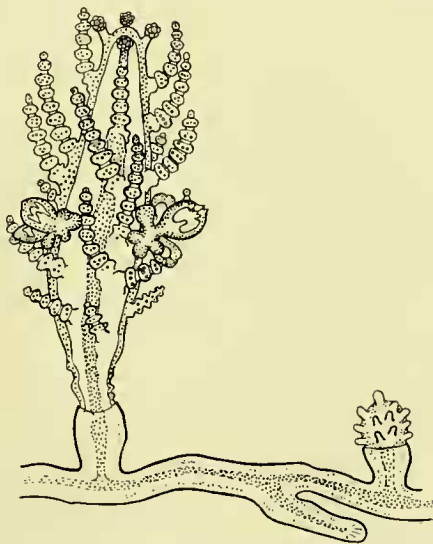


FIG. 3. *Asyncoryne ryniensis* Warren, a colonial hydroid with scattered moniliform body tentacles and an oral whorl of short capitate tentacles (redrawn from Warren, 1908).

later become colonial animals. This natural outcome of the adoption of a sedentary habit is an axiomatic principle which applies also to the Hydrozoa and it is therefore surprising that Kramp (1949) suggests that the solitary Corymorphidae are derived from colonial forms like *Asyncoryne* (Text-fig. 3). This is quite unlikely to have

taken place, a view already expressed by Totton (1954) "from general considerations".

We must therefore regard the solitary hydroid as being nearer the ancestral type, and, in considering capitate hydroids we have solitary forms in the Corymorphidae, the Tubulariidae, the Tricyclusidae, the Margelopsidae, the Acaulidae and the Myriothelidae, all the other families including the Corynidae being colonial.

As will be noted (p. 504) the hydromedusae are now generally believed to have either an actinuloid ancestor or to have descended from medusae having an actinuloid stage in their life history¹; these views are elaborated on pp. 503-506.

The actinula persists chiefly in the solitary hydroids and in its development the aboral whorl develops first, these tentacles corresponding to the medusa tentacles in Trachymedusae with a direct development. The oral whorl appears late in the development and is peculiar to the Hydroida.

I know of no primitive anthomedusan hydroid in which only the aboral whorl is present, all modern species having an oral whorl in addition. Two whorls of tentacles are found in the Corymorphidae, the Tubulariidae and the Margelopsidae and we can regard the Tricyclusidae, the Acaulidae and the Myriothelidae as more advanced because they have secondary whorls developed in the budding area between these primary whorls. We see the retention of this basic pattern of two whorls in some colonial forms, e.g., in one species of *Dipurena* and in *Cladonema radiatum*; they are also the first whorls to appear in the developing polyps of *Halocordyle* (*Pennaria*) and *Stauridiosarsia*.

In the three families with this basic tentacle arrangement (the Corymorphidae, the Tubulariidae and the Margelopsidae) the simplest kind of hydranth is found in the lower Corymorphines. In these forms there is no diaphragm in the hydranth and there are no stem canals or any of the elaborate features associated with the specialization we find in *Corymorpha nutans* and the Tubularians (see p. 499).

Examples of the modern survivors of this early Corymorphine condition are *Hypolytus peregrinus* Murbach, *H. obvoluta* Kramp and *Euphysa aurata* Forbes. In the first two both whorls are moniliform, that is, the nematocyst batteries are grouped like so many beads on a string, which allows the tentacle to be highly contractile.

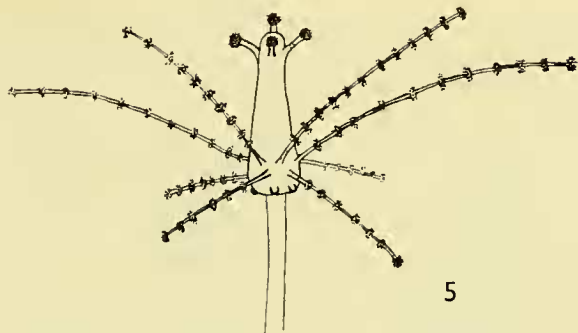
The moniliform condition exists also in the medusae of *Euphysa* and *Corymorpha* and also in a degenerate condition in those of a great many species of medusae (but see p. 492 for details of these) and I am inclined to regard this type of moniliform tentacle as very primitive and inherited unchanged from a medusoid ancestor. Even in the hydroids *Hypolytus peregrinus* (Text-fig. 4) and *H. obvoluta*, the oral tentacles are much shorter than the aboral ones and this condition leads on to the short capitate tentacle retaining only a single knob as in the hydroid *Euphysa aurata* (Text-fig. 5).

This is probably the way in which the short capitate tentacle originated and this type of tentacle is characteristic of the oral whorl occurring either in the larval or adult hydroid of the Corymorphidae, the Tubulariidae, the Margelopsidae, the

¹ Here I have not considered remoter ancestors, so that the theories of Hadzi (1944) and Jägersten (1955) concerning bilaterally symmetrical metazoan ancestors lie outside the scope of this paper.



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FIG. 4. *Hypolytus peregrinus* Murbach, a solitary Corymorphine with moniliform tentacles in both oral and aboral whorls (after Murbach, 1899).

FIG. 5. *Euphysa aurata* Forbes, a solitary Corymorphine in which the oral whorl is capitate and the aboral whorl is moniliform; hydranth of a young polyp. with tentacles fully extended (after Rees, 1937)

Tricyclidae, the Acaulidae, the Myriothelidae and in all the colonial capitate hydroids. As a basic type of tentacle it becomes duplicated on the body of the hydranth in the inter-whorl area in a large number of families.

To return to the moniliform tentacle it appears that the aboral tentacles of *Euphysa* and *Hypolytus* hydroids have been retained in their primitive form only because the feeding habits of the hydroids favour the retention of the very long extensile fishing tentacle of the medusa. In these hydroids the tentacles are extended radially over the soft mud to trap any organism creeping over them. With the adoption of firmer substrata, the tentacles lost their need to be very extensile, this permitting a scattering of nematocyst armature and the evolution of a stouter, more rigid, and less contractile tentacle. This, the filiform type, is the aboral tentacle we have in *Corymorpha nutans*, the Tubularians, the Halocordylidae (Pennariidae) and the Acaulidae, and in vestigial form in the Corynidae.

The moniliform arrangement still persists in aberrant survivals like the colonial hydroid *Asyncoryne ryniensis* Warren (Text-fig. 3) in which the aboral moniliform tentacles have become scattered over the body of the hydranth perhaps as a result of the lengthening of the body of the hydranth itself. In the solitary hydroid, *Tricyclus singularis*, they persist only in a very imperfect form (Text-fig. 6). Both these forms could have arisen along independent lines from an *Euphysa*-like ancestor (see p. 514).

Euphysa thus represents, as regards the hydranth, a basic type from which several evolutionary lines can be traced. The higher Corymorphines (like *Corymorpha nutans*), the Margelopsidae and the Tubulariidae, although not arising directly from an Euphysid could be derived from a descendant through partial disappearance of the nematocyst battery on the oral tentacles and the evolution

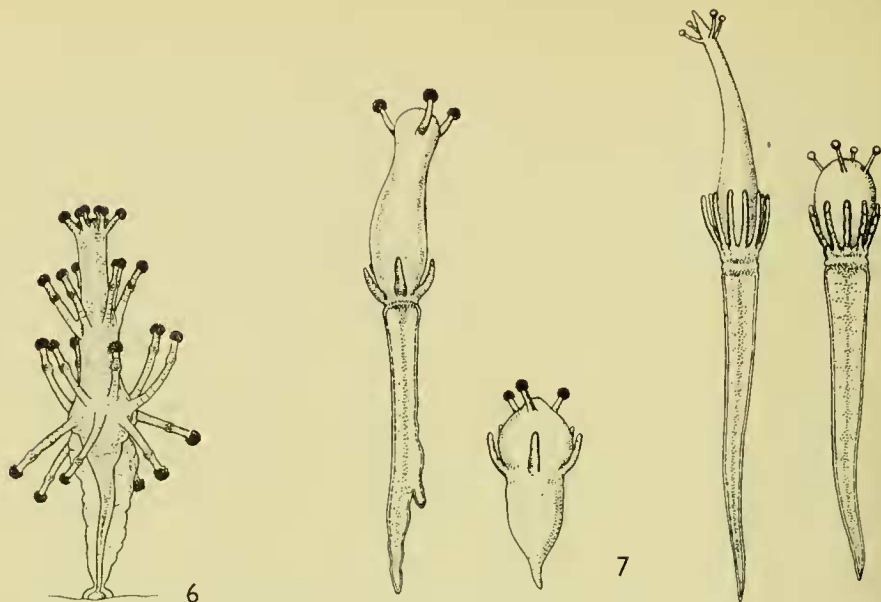


FIG. 6. *Tricyclusa singularis* (Schulze), an aberrant solitary capitate hydroid in which the moniliform arrangement of nematocysts persists in an imperfect form (redrawn after Vervoort, 1947).

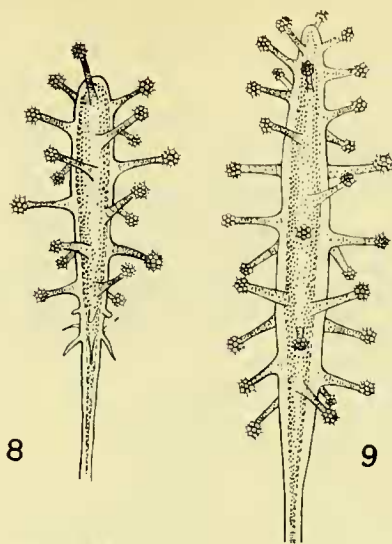
FIG. 7. *Corymorpha nutans* M. Sars: planktonic larval polyps with capitate oral tentacles and filiform aboral ones (after Hartlaub, 1907).

of filiform tentacles in the aboral whorl. There are also secondary changes due to elaboration, size, and the influence of habitat that need not concern us at this point.

This intermediate Corymorphine may have been something like the larval *Corymorpha nutans* with its capitate oral tentacles, its filiform aboral tentacles and the absence of a diaphragm (Text-fig. 7). Such a form could be envisaged as an unspecialized ancestor which could be the starting point for other evolutionary lines, viz.:—elaboration of the solitary form culminating in *Myriothele*, and also in the development of a colonial habit as in *Coryne*.

If we consider only the hydroid of *Cladonema* (leaving its highly evolved medusa out of consideration) we have here in the form of the polyp (Pl. 12, fig. 1) the simplest type of colonial hydroid from which the colonial Corynoidea (except the Asyncorynidae and the Cladocorynidae) are evolved (see p. 514).

It has not been generally realized that in some Corynidae, the primary hydranths of a colony regenerating after a period of dormancy are different from later secondary or tertiary hydranths. In *Staurocoryne filiformis* the first polyp has well developed filiform tentacles, but secondary ones have vestigial ones and they may disappear completely in tertiary polyps (Text-figs. 8 and 9). Hartlaub (1895), to judge from his figures, seems to have encountered the same phenomenon in *Stauridiosarsia*



FIGS. 8 and 9. *Staurocoryne filiformis* Rees: (8), primary polyp from a regenerating stolon (after Rees, 1936); (9), fully developed hydranth of three months old colony (original). Note the disappearance of the filiform tentacles.

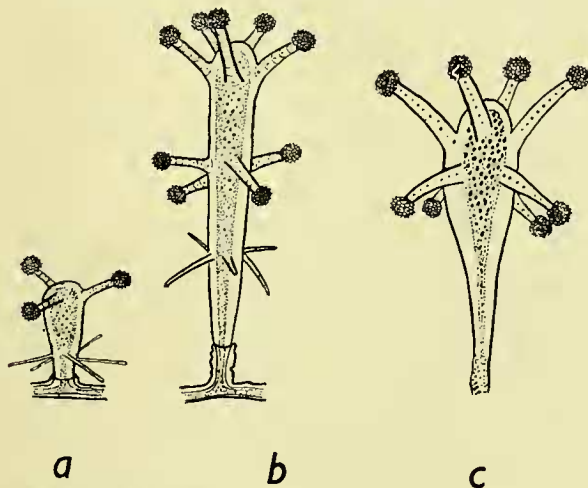


FIG. 10. *Stauridiosarsia producta* (Wright): a-c, loss of filiform tentacles; a, developing polyp with two primary whorls; b, fully developed polyp with filiform tentacles (both after Rees, 1938); c, polyp without filiform tentacles (redrawn after Hartlaub, 1895).

producta (Text-fig. 10, a-c) and these changes may represent the general trend towards the loss of the filiform tentacles in the Corynidae.

At one time a miscellaneous assemblage of corynids, corymorphines and tubularians were grouped together either with *Halocordyle* (*Pennaria*) in the Halocordylidae or with *Cladonema* in the "Stauridiidae" because of the possession of these filiform tentacles (in association with an oral whorl of capitate tentacles), but this kind of arrangement persists only in out-of-date classifications like those of Fraser (1944).

From the basic type of Corynoid hydranth the typical Corynid has been evolved by the addition of whorls of short capitate tentacles; these are in whorls in some primary polyps, becoming scattered in later polyps. Side by side with this development the filiform or "false" tentacles tend to disappear.

Sometimes the filiform tentacles disappear completely leaving only an oral whorl of capitate tentacles as in *Hydrocoryne miurensis* and *Cladonema myersi* (Text-fig. 11).

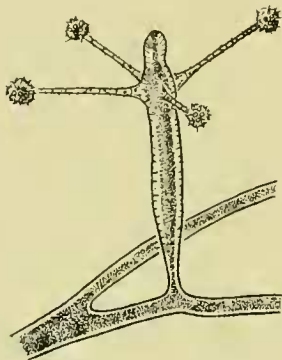


FIG. 11. *Cladonema myersi* Rees: the filiform tentacles have disappeared in this species of *Cladonema* leaving only the oral capitate whorl (after Rees, 1950).

The early naturalists regarded the higher Corymorphines and the Tubularians as the highest evolved and most elaborate of the gymnoblastic hydroids. This is true in so far as we can regard them as representing the greatest elaboration of the solitary hydroid and the metabolic activity of a large polyp must approach that in many a well developed colonial form (Text-fig. 12). The most noticeable feature is the large size of these large polyps (*Corymorpha nutans* goes up to 11.4 cm. in length and *Branchiocerianthus imperator* up to 224 cm.). This implies, and there are, structural modifications which accompany gigantism, for example, the special cushion ring (diaphragm) of parenchyma at the base of the aboral whorl of tentacles, the parenchyma and canals in the stem, the very large number of rooting filaments, the large number of tentacles and the increase in the budding zone by the expansion of this area into long, hollow, branching blastostyles. *Branchiocerianthus*, itself, with its bilateral symmetry may be further modified for feeding in a current.

The solitary polyps of the Acauloidea (see p. 515) proceeded along a different line from the erect Tubularoids, and the failure to develop a proper hydrocaulus (as will be noted on p. 466) may be associated with the feeding habits of the myrio-

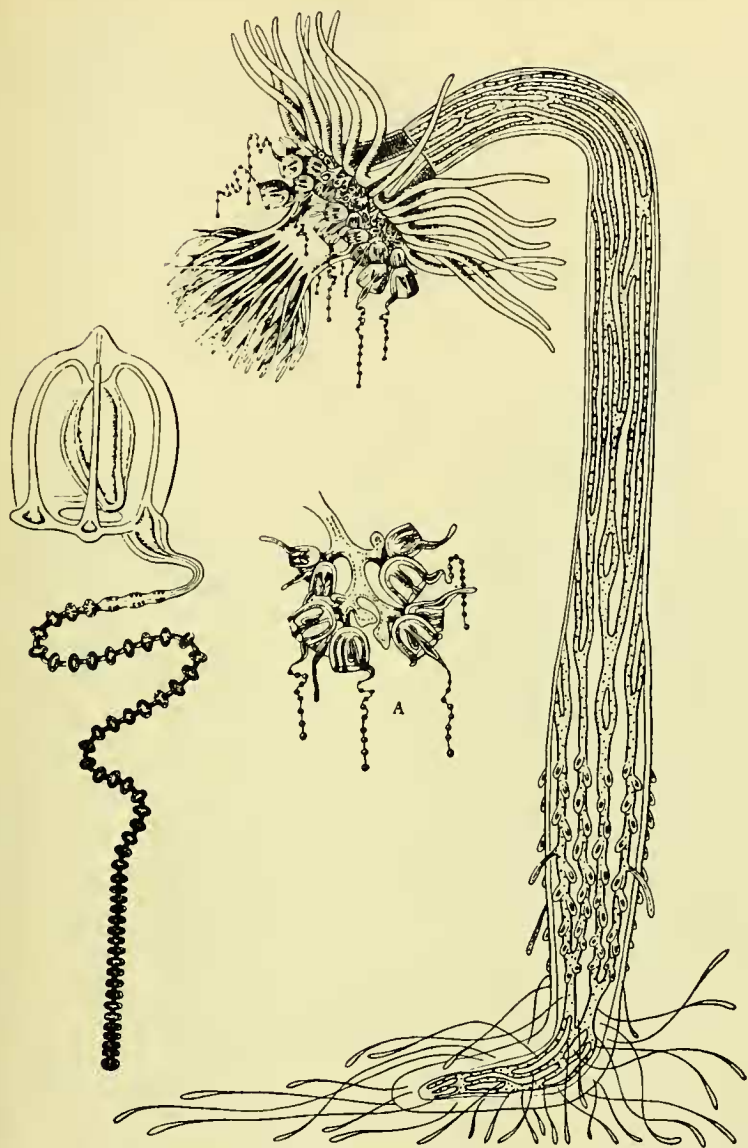


FIG. 12. *Corymorpha nutans* M. Sars, an elaborate solitary hydroid (after Allman, 1872).

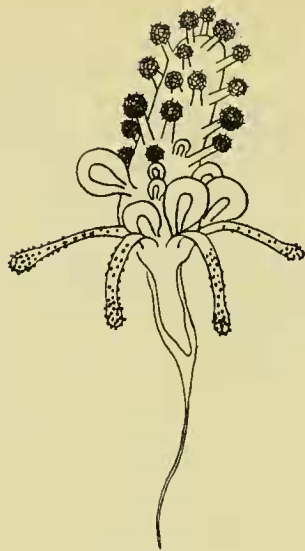
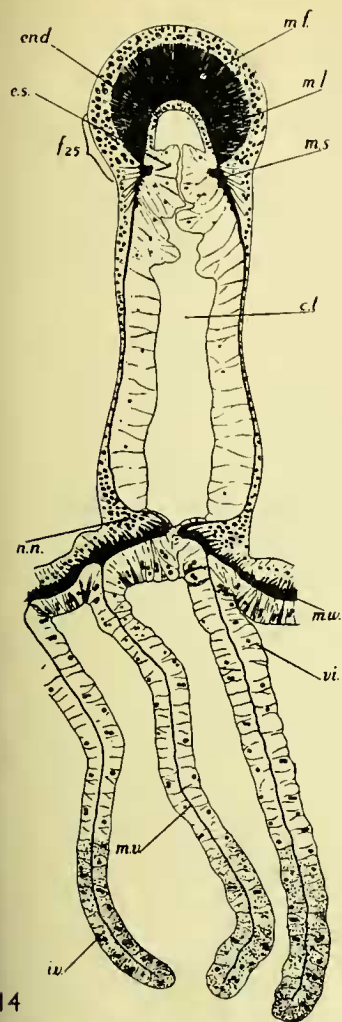


FIG. 13. *Acaulis primarius* Stimpson: young polyp with male gonophores (redrawn after Hyman, 1940). Note the gelatinous tube and anchoring filaments as in *Euphysa*, and the multiplication of short capitate tentacles in the intertentacular area.

theline polyp. *Acaulis* is but little removed from the mud-dwelling, primitive Corymorphine but the tendency to become vermiform is already apparent in the lengthening of the hydranth and the multiplication of capitate tentacles in the intertentacular area (Text-fig. 13). This tendency to elongate the polyp and consequent enormous multiplication of the number of short capitate tentacles on the body of the hydranth culminates in the highly specialized myriothelines where there are single polyps up to 30 cm. in length (*Myriothela austrogeorgiae* Jäderholm, 1905). Associated with this elaboration is an increase in the endodermal absorptive surfaces by the development of endodermal villi (Text-fig. 14). The fixed gonophores are borne on the body of the hydranth in some species, while in others special coryniform tentacles are developed and these are transformed into blastostyles (Text-fig. 15).

Great importance was attached to the presence of the supporting lamella in *Coryne* and tubularoid hydroids by Kramp (1949) who regarded continuity of the mesogloeal lamella, separating the endoderm of the hydranth from that of the tentacle as a primitive feature. It seems to have influenced him in developing his theory of a *Tubularia* line and a *Corymorphia* line in the Capitata.

It has not been possible to follow up this idea concerning the supporting lamella as fully as could be wished in this paper. The hydroid *Euphysa aurata* has however been thoroughly examined from excellent serial sections kindly given to me by Dr. Jöran Hult in 1939. There is no doubt that the lamella is continuous, separating



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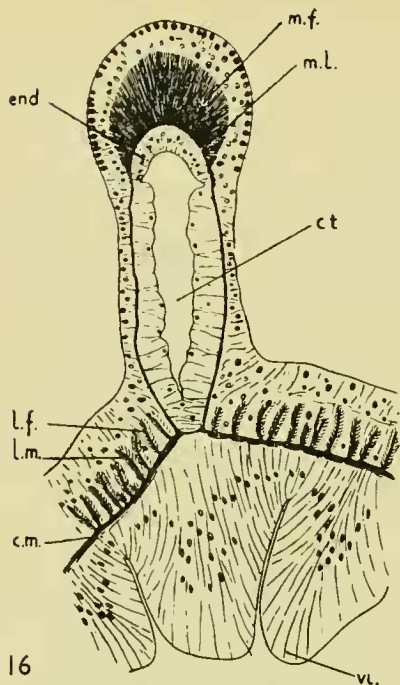
FIG. 14. *Myriothela penola* Manton: transverse section of hydranth body, showing endodermal villus (after Manton, 1940).

FIG. 15. *Arum cocksii* Vigurs, an elaborate Myriotheline hydroid (after Allman from Hyman, 1940): (1), anterior portion with capitate body tentacles; (2), clasper; (3), coryniform blastostyles; (4), ripe eggs held by claspers; (5), actinula being released; (6), perisarc-covered stem with modified anchoring filaments.

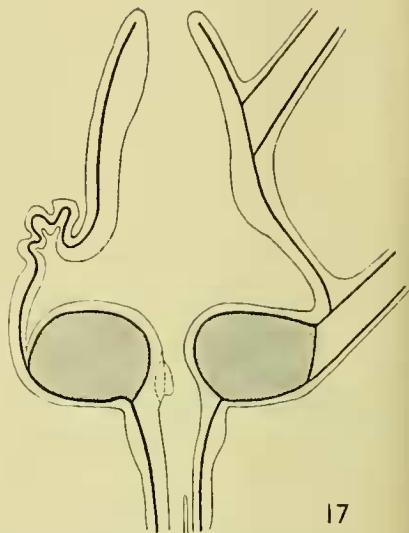


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off the endoderm of the capitate tentacles in the oral whorl, but in the aboral moniliform whorl the lamella is interrupted (or as Kramp states, the supporting lamella



16



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FIG. 16. *Myriothele capensis* Manton: diagrammatic transverse section of a body tentacle and body wall to show the continuous mesogloea across the base of the tentacle; *ct.*, endodermal cavity of tentacle; *c.m.*, circular muscle process; *end.*, endoderm; *l.f.*, longitudinal mesogloea flanges projecting into ectoderm; *l.m.*, longitudinal muscles inserted on to mesogloea fibrils; *m.f.*, apical pad of mesogloea fibrils; *m.l.*, basal layer of solid mesogloea; *vi.*, endodermal villus (after Manton, 1940).

FIG. 17. Diagrammatic representation of the hydranth of *Tubularia* in longitudinal section showing the parenchymatous cushion (shaded) and the mesogloecal lamella (heavy black line) (redrawn from Grönberg, 1898).

is absent). Manton (1940) gave an excellent figure of the continuous lamella in the short capitate tentacle in *Myriothele capensis* (Text-fig. 16) and Kramp stated that the same condition prevails in the typical Corynids where the tentacles are also all short capitate ones.

It is possible to hold the view that the lamella continues intact across the base of the tentacle, only when that tentacle is a small structure, and we must remember that the short capitate tentacle develops without much local disturbance of tissue. There is, however, considerable local disturbance of the body wall during the formation of the larger aboral tentacles and the lamella may never be repaired subsequent to the formation of this type of tentacle. In other words, the presence or absence of a supporting lamella may bear a direct relation to the size of the tentacle developed.

In *Tubularia*, Grönberg (1897, pl. 4, fig. 1) has shown that the lamella, associated with the parenchymatous cushion, cuts off the endoderm of the tentacles (Text-fig. 17), but this seems to be a secondary development associated with the form of the cushion in *Tubularia* and may not be a primary feature as believed by Kramp. Enough has been said to indicate that the supporting lamella may be found to have little significance in classification when it is investigated more fully.

In the higher Corymorphines (such as *Corymorpha nutans*) there is a gastric diaphragm which divides the cavity of the hydranth into an oral and an aboral

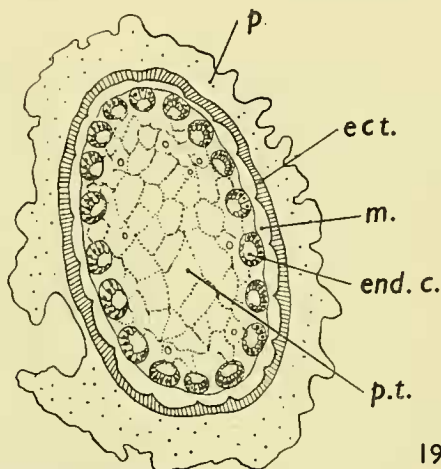
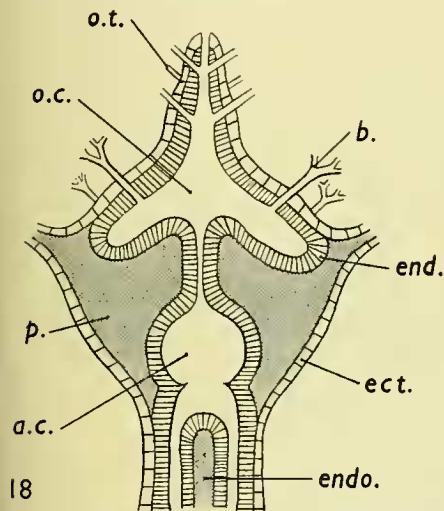


FIG. 18. Diagrammatic longitudinal section of the hydranth of *Corymorpha nutans* (redrawn after Allman, 1872); it will be noted that the diaphragm is not reduced as in *Tubularia* (Fig. 17) and that the endoderm of the hydranth is continuous with that of the tentacle: a.c., aboral chamber; b., blastostyle; ect., ectoderm; end., endoderm; endo., endocord; o.c., oral chamber; o.t., oral tentacle; p., parenchyma.

FIG. 19. Diagrammatic transverse section of the stem of *Corymorpha nutans* showing parenchyma and peripheral endodermal canals (redrawn after Stechow, 1909): ect., ectoderm; end.c., endodermal canals; m., mesogloea; p., gelatinous perisarc; p.t., peritreme.

chamber (Text-fig. 18) and the stem of the hydranth is filled with parenchyma except for a series of peripheral canals representing the original cavity (Text-fig. 19). Primitive Corymorphines of small size do not possess this diaphragm which is also found in a modified form in *Tubularia*. This diaphragm is of great interest to students of phylogeny in Siphonophores but as regards the Corymorphines and Tubularians its origin seems to me to be linked with the large size reached in the polyp of these forms. Although it later acquired a more specialized function it must have originated as a thickening of the hydranth wall to support a large whorl of tentacles and the same cause (i.e., a large hydranth head) necessitated a stiffening of the polyp stem resulting in the so-called "endocord" of Garstang (1946, p. 124, fig. 18).

There is a slightly different arrangement in *Tubularia* where the posterior chamber has been eliminated and what remains of the stem canals open through a sieve plate

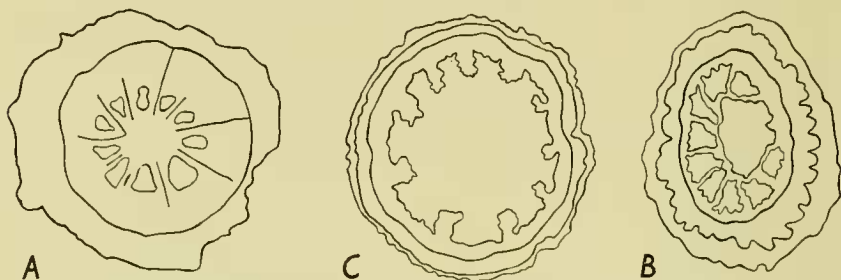


FIG. 20. Degeneration of the stem canals in *Tubularia* (simplified from Grönberg, 1898): A, sieve plate; B and C, transverse sections of stem.

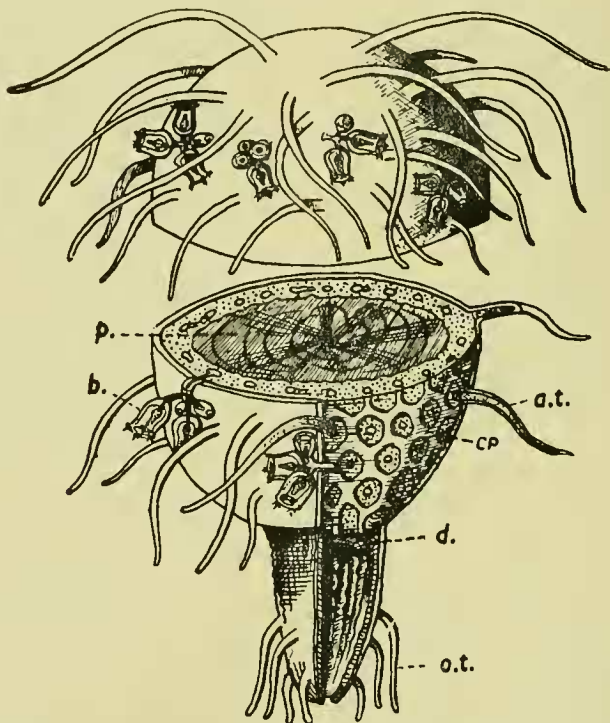


FIG. 21. *Pelagohydra mirabilis* Dendy (after Garstang, 1946); the lettering has been changed to conform to the interpretation given in this paper: a.t., aboral tentacle; b., blastostyles with developing medusae; d., diaphragm; o.t., oral tentacle; p., parenchyma.

into the oral chamber (Text-fig. 20). The atrophy of the stem canals, inherited from a Corymorphine ancestor, in *Tubularia* may be associated with the development of a firm perisarc and with the much smaller diameter of the stem.

Garstang (1946, p. 126 and p. 184) follows Dendy in interpreting the swollen aboral end of the pelagic hydroid *Pelagohydra* as "the stalk region or hydrocaulus, with its axial parenchyma and peripheral labyrinth of canals", which, "has been dilated to form a kind of float and the hydranth with its oral tentacles is reduced". This interpretation led Garstang into difficulties in his digressions into hydroid phylogeny. In all Tubularian and Margelopsid hydroids the gonophores are situated in the inter-tentacular region and I do not think that *Pelagohydra* is any exception (Text-fig. 21). Thus the float could be a dilated and much modified hind end of the hydranth in which the posterior whorl of tentacles and the ring of blastostyles have become scattered due to the swelling of this part of the hydranth into a float. Garstang homologized the canals in the float with the canals in the stem of *Corymorpha* but I do not think this is the right interpretation for as has been said, it implies that the float is cauline in origin. On the interpretation adopted here the float is the basal half of the hydranth in which the parenchyma supporting the diaphragm is enormously developed, eliminating not only the posterior (aboral) chamber but also almost completely obliterating the posterior half of the oral chamber leaving only canals for feeding the tentacles and the blastostyles.

Grönberg (1897, Taf 4, figs. 1 and 3) figures these canals in *Tubularia*, although

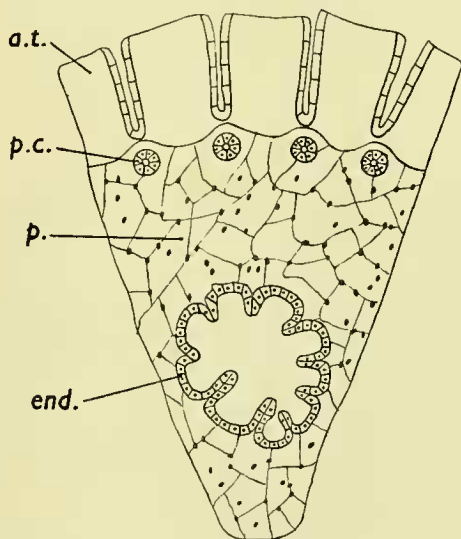


FIG. 22. Diagrammatic transverse section of a segment of the hydranth of *Tubularia* showing the peripheral canals which are continuous with the oral chamber of the hydranth (simplified from Grönberg, 1898): *a.t.*, aboral tentacle; *end.*, endoderm; *p.*, parenchyma; *p.c.*, peripheral canals.

Garstang does not seem to have noticed them (Text-fig. 22), and in his conclusions derives both the Tubulariidae and the Monocaulidae (i.e., *Branchiocerianthus*) from the Corymorphidae. In fact the structure of *Branchiocerianthus imperator*, described by Miyajima (1900) becomes intelligible when we relate it to that in *Corymorpha nutans*. At one stage in the evolution of *Branchiocerianthus* (Text-fig. 23), the diaphragm must have been so closely adpressed to the intertentacular wall

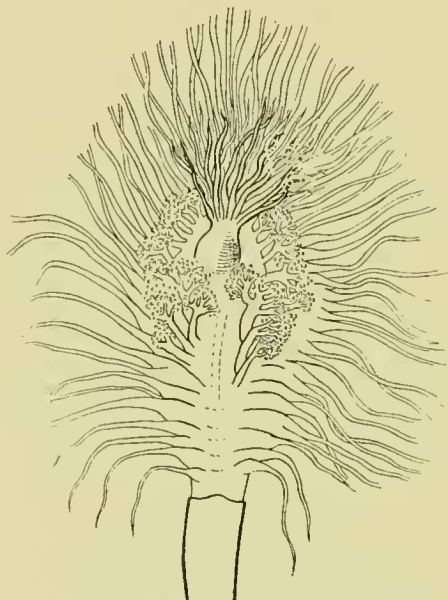


FIG. 23. *Branchiocerianthus urceolus* Mark: Oral face of bilaterally symmetrical polyp (simplified from Mark, 1898).

of the hydranth by the development of the parenchymatous cushion as to become fused with it, leaving only canals for feeding the blastostyles and the tentacles (Text-fig. 24). Although Mark (1898) mistook this large hydroid for a Cerianthid, his remarks on these canals confirm the view that they are food canals: "Radial canals are traceable running across the disk from the base of the oral tube to the bases of the marginal tentacles, before reaching which many of them fork, each of the branches communicating with the lumen of a single tentacle". In these species the aboral chamber has become large, possible due to the disappearance of most of the parenchymatous tissue (Text-figs. 23 and 24).

On the assumption that the float of *Pelagohydra* is cauline in origin, Garstang goes on to say (p. 184), "It is thus possible to imagine the sessile forebears of *Pelagohydra* as solitary Tubularias or Corymorphas, owing to the basal position of their gonophores and simple heads. There must have been—and may still be—a

tribe of tall, simple, naked polyps rising from a creeping stolon with gonophores on their basal stalks, supported only by an endochordal axis; and this tribe was presumably ancestral not only to *Pelagohydra*, but to all "Tubularians". Here it appears that Garstang was deceived by the secondary simplification of many colonial hydroids into deriving solitary forms from colonial ones. The example which he quotes, *Gemmellaria* (*Zanclaea*) and *Clavatella* (*Eleutheria*), are among the highest evolved forms in the Capitata. Similarly the erroneous suggestion that the gonophores were originally cauline (instead of being intertentacular in origin) is adequately treated on p. 471.

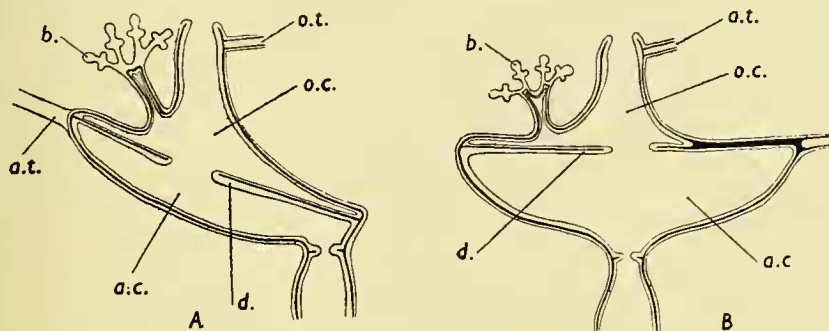


FIG. 24. *Branchiocerianthus imperator* (Allman): hydranth redrawn from Miyajima (1900): A, diagrammatic sagittal section; B, diagrammatic transverse section: a.c., aboral chamber; a.t., aboral tentacle; b., blastostyle; d., diaphragm; o.c., oral chamber; o.t., oral tentacle.

Garstang however came near to my own views at many points in his remarkable survey, for instance, "Without *Corymorpha* the structure of *Tubularia* would be unintelligible, and no one would suspect the secondary simplification which has led to *Pennaria*". If he had realized the simplicity of the lower Corymorphines like *Euphysa* (*Corymorpha annulicornis*), and been less preoccupied with "cauline" gonophores in *Pelagohydra*, he would have recognized the significance of these forms in the phylogeny of *Corymorpha*, *Tubularia*, *Acaulis* and *Myriothele*.

Concerning *Myriothele* (*Arum*), Garstang (p. 145) seems to have erred in assuming that the branched coryniform blastostyles are vestiges of a once fully colonial life. These branched blastostyles are more likely to represent elaboration (often associated with large-sized polyps) in a solitary polyp, for the *Myriothele* line can be traced back through forms like *Acaulis* to a primitive Corymorphine (and all are solitary forms). The large egg and its unique clusters indicate a high degree of specialization in *Arum cocksii* (Text-fig. 15 p. 467).

It is not proposed to enlarge on the codonid relationships of the Disconanth Siphonophora here; these have been discussed by Totton (1954) and Picard (1955).

(b) *Division of labour in a colonial system*

Once the hydroid became a colonial form, the transport of food from polyp to polyp was assured by the continuous coenosarc. Among the many advantages it meant that the individual polyp need not be so large and could undergo secondary simplification. This is what I believe has happened in the deceptively simple polyps of the Corynidae where a large number of identical polyps carry on the function formerly undertaken by a solitary polyp.

The loss of the long aboral tentacles in the typical Corynids may be associated with the development of a bushy colonial habit where the long aboral tentacles could not be manoeuvred successfully. On the other hand they are retained in the Halocordylidae (Pennariidae) where the pinnate branching and the positioning of the hydranths allow these tentacles full play (Text-fig. 25).

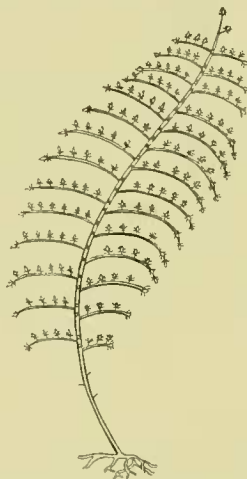


FIG. 25. The arrangement of hydranths on the upright, branched hydrocaulus of *Halocordyle* (*Pennaria*).

The colonial system, too, meant the beginning of specialization for particular tasks. In the Corynidae, which we may regard as among the simpler forms of colonial capitate hydroids, the polyps are all alike and perform the same functions, and it is only among the higher forms of corynoid polyps that we see this division of labour setting in. Some evidence for this differentiation was reported by Russell and Rees (1936) in the polyps of *Zanlea costata* Gegenbaur where it was noticed that there was some indication of division into nutritive and reproductive polyps, but it was also evident that towards the end of the budding period the nutritive polyps might also be transformed into reproductive ones.

Division of labour in the polyp has not progressed in the Capitata as a whole but in *Ptilocodium* and the Solanderiids some progress has been made. In *Ptilocodium*

there are two kinds of polyps, the nutritive zooid (unarmed and without tentacles) which also bears the gonophores, and the dactylozooid or defensive zooid. The ordinary polyp no longer carries the gonophores and these are situated on the rhizocaulome formation in the Solanderiids like *Dendrocoryne*.

It is only when the more advanced Filifera are considered that we find the best examples of division of labour, where the different functions of feeding, budding of gonophores and protection, each have their own special kind of polyp. *Hydractinia echinata* (Fleming) is the classical example with nutritive, reproductive and two kinds of defensive zooid.

3. THE POSITION OF THE GONOPHORES

The position of the gonophores is, I believe, of limited significance in assessing whether a particular hydroid is primitive or advanced, but reflects general trends

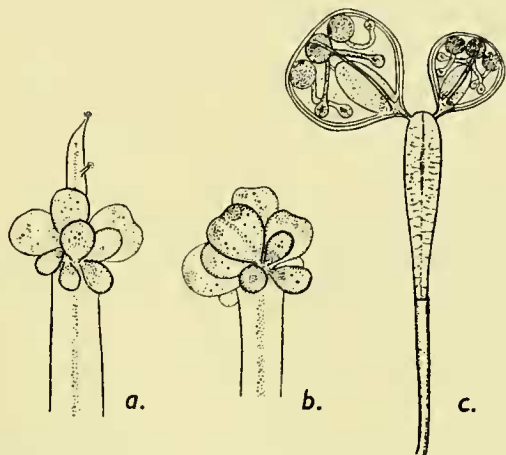


FIG. 26. Reduction of hydranths to blastostyles: A and B, *Zanlea costata* Gegenbaur; c, *Dipurena hallerata* (Forbes) (after Russell & Rees, 1936; Rees, 1939).

in the group. The position of the budding area between the two main whorls of tentacles on the body of the hydranth is one of the most constant (and essentially primitive) features of capitate hydroids. This position is the same in the primitive solitary hydroid and in the ancestral medusoid; as a budding area it involves no food transport problems because the food is either transferred direct through the wall of the stomach or passes into the lumen of the blastostyle which is in direct continuity with the stomach.

There are however some serious disadvantages even though there are no food transport problems. When the hydranths are fertile and producing medusae or fixed gonophores in abundance (as they usually do in favourable circumstances) the hydranth itself becomes reduced to a simple blastostyle, without mouth or tentacles, due to reproductive exhaustion (Text-fig. 26). It means that most of the polyps of the colony must die down and become reorganized once more as

TABLE I.—Position of Gonophores in the Filifera

	On all hydranths	On selected hydranths	On special hydranths	On stem below hydranth	On stems	On stolons
Family Clavidae						
<i>Clava squamata</i> (O. F. Müller)
<i>Merona cornucopiae</i> (Norman)	.	..	×
<i>Cordylophora lacustris</i> (Pallas)	×
<i>Turritopsis nutricula</i> Brooks	×	..
<i>Rhizogeton fusiformis</i> L. Agassiz	×
Family Hydractiniidae						
<i>Podocoryne carnea</i> M. Sars
<i>Hydractinia allmani</i> Bonnevie	.	×
<i>Hydractinia echinata</i> (Fleming)	.	..	×
Family Cytaeidae						
<i>Cytaeis japonica</i> Uchida	×
Family Bongainvilliidae						
<i>Dicoryne conferta</i> (Alder)	.	..	×
<i>Heterocordyle conybearei</i> Allman	.	..	×
<i>Bongainvillia linearis</i> Alder	×
<i>Bongainvillia muscoides</i> (M. Sars)	×	..
<i>Garveia nutans</i> Wright	×	..
<i>Aselomaris arenosa</i> (Alder)	×
<i>Rhizorhagium rosetum</i> (M. Sars)	×
Family Endendriidae						
<i>Endendrium ramosum</i> (L.)
<i>Endendrium capillare</i> (Alder)	.	..	×
Family Pandaeidae						
<i>Leuckartiara octona</i> (Fleming)	×	×

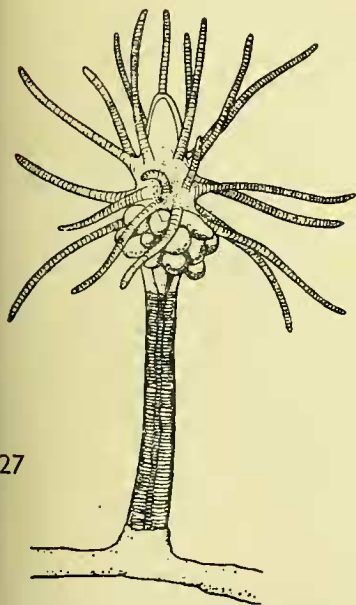
feeding polyps. Usually this involves an almost complete cessation of activity for many days. In high latitudes, for instance, this must curtail the already short breeding period in species near the temperature limit of their distribution.

Except in the aberrant Solanderiidae where the gonophores are not sited on the hydranth, most capitate hydroids conform to the above pattern. In *Eleutheria* (Text-fig. 48, page 500) and *Hydrocoryne* (Text-fig. 49, page 500), however, the gonophores have moved towards the base of the long polyps of these species, some distance from the chief digestive area.

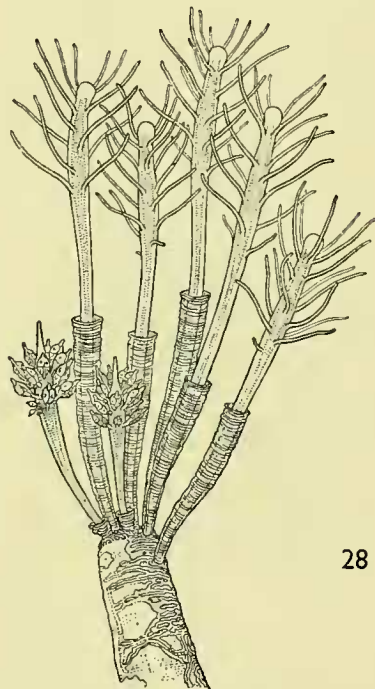
In theory, at least, the adoption of a colonial habit, with stolonization and an erect hydrocaulus, would also mean the evolution of an efficient means of circulating food throughout the colony, so that it would no longer be necessary for the budding area to be in the immediate vicinity of the point of ingestion of food.

Except in some aberrant forms already mentioned, the Capitata have progressed little in this direction and it becomes necessary to choose examples from the Filifera.

The change in the position of the gonophores away from the hydranths is a general trend in the Filifera which is best illustrated in a table which gives examples of the different positions in which they are found (Table I).



27



28

FIG. 27. *Clava squamata* Müller: gonophores are borne on all hydranths (after Vervoort, 1946a).

FIG. 28. *Merona cornucopiae* (Norman): nutritive and reproductive polyps are distinct from each other (after Rees, 1956).

In the Clavidae, one of the more primitive families of the Filifera, we find nearly all the steps in the transfer of the gonophores away from the hydranths. In *Clava squamata* all the hydranths bear gonophores (Text-fig. 27), but in *Merona cornucopiae*, division of labour has set in; the nutritive polyps are able to concentrate on non-reproductive functions (Text-fig. 28). In *Cordylophora lacustris* the reproductive polyp has disappeared and the gonophore is borne directly on the hydrocaulus, a little way below the hydranth, and likewise, in *Turritopsis*, the medusa bud is borne directly on the hydrocaulus. (Text-fig. 29). Where there is little or no hydrocaulus the gonophore may be borne on the stolons as in *Rhizogeton fusiformis* (Text-fig. 30).

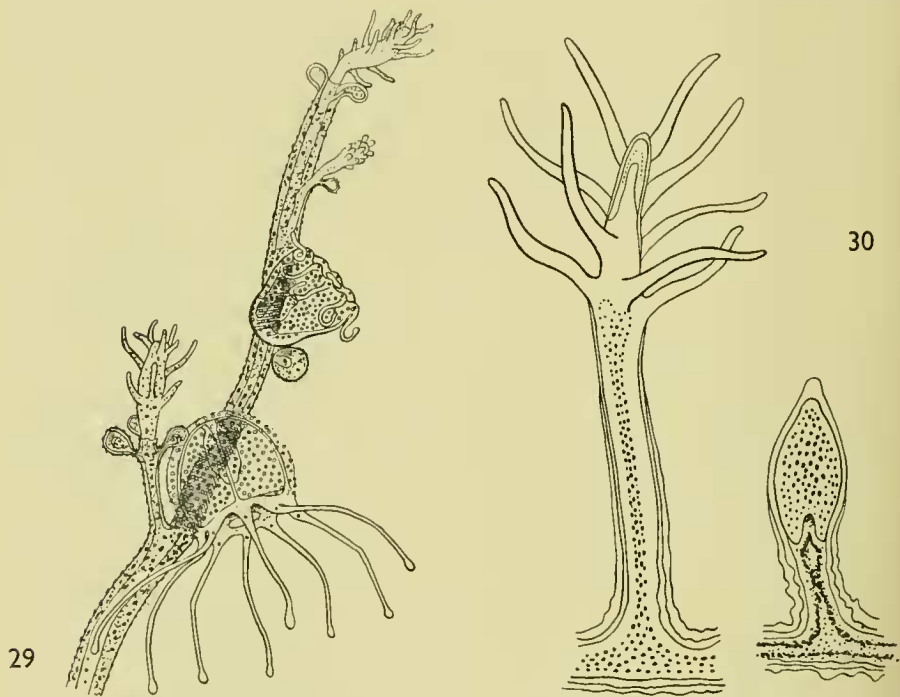


FIG. 29. *Turritopsis nutricula* Brooks: a colonial Clavid hydroid in which the medusa buds are borne directly on the hydrocauli (redrawn from Brooks, 1883).

FIG. 30. *Rhizogeton fusiformis* Agassiz: hydranth and polypoid male gonophores (simplified from Agassiz, 1862).

In the family Hydractiniidae there is a similar range of positions, although species like "*Stylactella*" *elsae-oswaldae* Stechow which have gonophores arising from the stolons have not been included in the table. Any nutritive polyp may become a reproductive one in *Podocoryne carnea*, but in *Hydractinia allmani* Bonnevillie it

appears that only a certain number of polyps bear gonophores (Rees, 1956*b*), these differing only in size from the nutritive hydranths (if we make some allowance for reproductive exhaustion). *Hydractinia echinata* on the other hand has specially evolved reproductive polyps and the ordinary nutritive hydranths never bear gonophores.

The family Cytaeidae, which in some respects is intermediate between the Hydractiniidae and the Bougainvilliidae, has gonophores borne directly on the hydrorhiza; in other respects, however, the family is not highly specialized (but see Rees, 1956*a*, p. 344).

In the higher groups of Filifera, only in a few members of the Eudendriidae like *E. ramosum* does the primitive condition, i.e., gonophores borne on the bodies of all the hydranths, persist, and even within this genus there is much diversity in their position.

In the other families, the Bougainvilliidae and the Pandeidae there are no surviving examples where gonophores are borne on the hydranths. Special reproductive hydranths comparable in function with those of *Hydractinia* are found in *Heterocordyle* and *Dicoryne* and these both have a specialized type of gonophore. In *Bougainvillia linearis* Alder (and also in *B. ramosa* and *B. superciliaris*), the budding area has moved away from the hydranth to the hydranth stalk which may carry several clusters of medusa buds. A more advanced condition is found in *Bougainvillia muscoides* where medusa buds are borne anywhere along the rhizocaulome formation (Rees, 1938).

Bougainvilliids with fixed gonophores exhibit a similar range of positions: *Aselomaris* (comparable with *B. linearis*), *Garveia* (with *Cordylophora*) and *Rhizorhagium* (with *Rhizogeton*).

These are only some of the examples which may be quoted but Table I demonstrates the evolutionary trend towards cauline gonophores, and it is also of considerable interest to note that individual species, within the same families and even the same genera, range from primitive to advanced positioning of gonophores. In this table the species which are considered to be the more primitive are placed at the top of the list and the more advanced towards the bottom of the list; this assessment being based on consideration of both the hydroid and its gonosome. What emerges from this Table is that although the siting of the gonophores shows a broad evolutionary trend in the groups, individual species even within the same genus have progressed at different rates—some retaining the primitive condition while others have reached various stages in the direction of simple gonophores arising directly from the coenosarc and the elimination of the special reproductive polyp. This represents a small part of the mosaic.

4. EGGS AND ENCYSTMENT

(a) *Lecithotrophic and Planktotrophic Larvae*

In the naked hydroids egg sizes vary greatly and in general it can be said that those of the solitary forms are large while those of the colonial species exhibit a marked tendency to be small.

The large lecithotrophic eggs of *Corymorpha nutans* are typical; they are few in number, amoeboid and develop at the expense of nurse eggs on the manubrium. When the egg is finally cast out it may already have been fertilized and have secreted a thin pellicle around itself. Such eggs are 0.26–0.28 mm in diameter.

In *Hybocodon prolifer* the eggs are also large, amoeboid, and feed on nurse eggs but here they remain attached to the manubrium until they develop into quite large actinulae. *Tubularia* too for all practical purposes may be regarded as a solitary hydroid and here also in the sporosacs we find the development of a few actinulae at the expense of the other eggs. Actinulae are also found in at least one Corynoid (*Actigia pusilla*) and in *Myriothele cocksi* there is an elaborate actinuloid larva; here the ripe egg is held by special "claspers" until the actinula reaches full development—this is the greatest degree of brood protection found in capitate hydroids.

The case is rather different in *Margelopsis haeckeli* where the larva develops into an actinula-like hydroid before being released from the manubrium of the medusa. In this species the eggs are thought to be parthenogenetic as no male gonads have ever been seen; this type of reproduction takes place in the summer. Later larger eggs are produced which develop as far as the stereoblastula stage on the manubrium and are then released, to settle on the bottom, becoming covered by a thin dome-shaped periderm; they are regarded as resting stages (Werner, 1954).

Eleutheria dichotoma, which may be regarded as an aberrant colonial Corynoid, has a specialized cavity or brood pouch in the medusa where the small, non-amoeboid eggs develop into the planula stage. A similar sac has been reported in little known "Pteronemid" genera of medusae (*Pteronema*, *Ctenaria* and *Dendronema*).

In many of the Corynidae with well developed colonial habit, the eggs are usually small and develop into planulae after release from the sporosac or medusa. Brood protection in capitate hydroids thus reaches its highest development in the solitary forms but occasionally, as already noted, protection as far as the actinula stage is found in some colonial forms.

In the higher groups of Anthomedusae other than those with capitate hydroids we find surprisingly little by way of protection of brood. In the Clavidae, *Turritopsis*, for instance, retains the eggs on the manubrium of the medusa until they swim away as planulae and the same degree of protection is found in the fixed gonophores of some Bougainvilliid hydroids (e.g., *Aselomaris michaeli* Berrill, 1948).

The eggs of many Bougainvilliid medusae and related families are often quite small, numerous and develop after being shed into the water.

Typical egg sizes are noted in Table II opposite.

It has already been noted that as a rule the solitary hydroids have large yolk eggs, some measure of brood protection, and they frequently develop into an actinula, which, when it leaves the parent (hydroid or medusa) is ready to settle on the bottom. This can almost be termed non-pelagic development for the actinula's free existence in the plankton must be of very short duration.

By contrast, the smaller eggs (0.15 mm. or less in diameter) of most colonial athecate hydroids and medusae may be shed into the water as fertilized eggs or less

TABLE II.—*Egg Sizes in Anthomedusae and their Hydroids*

(Measurements in mm.)

HYDROIDS WITHOUT A MEDUSA PHASE

Solitary forms

Tubularia crocea Agassiz, 0.55 (Berrill, 1952).*Acaulis primarius* Stimpson, 0.2–0.25 (Berrill, 1952).

Colonial forms

Hydractinia echinata Fleming, 0.15–0.2 (Berrill, 1953).*Aselomaris michaeli* Berrill, 0.1–0.12 (Berrill, 1948).

MEDUSAE

Solitary forms

Corymorpha nutans M. Sars, 0.26–0.28 (Rees, 1937a).

Colonial forms

Stylactis hooperi Sigersfoos, 0.1–0.12 (Berrill, 1953).*Lizzia blondina* Forbes, 0.08–0.12 (Rees, unpublished).*Rathkea octopunctata* (M. Sars), 0.14 (Rees and Russell, 1937).*Bougainvillia britannica* Forbes, 0.14–0.15 (Russell, 1953).*Bougainvillia superciliaris* (Agassiz), 0.13 (Berrill, 1949).*Amphinema dinema* (Péron and Lesueur), 0.14–0.15 (Rees and Russell, 1937).

frequently they may be retained on the manubrium or spadix until the planula stage is reached. On the assumption that the planula takes about two days to develop and may remain planktonic for a further two or three days, a free larval life of 4–5 days is envisaged.

Thorson (1950, p. 11) gave a fine account of the various types of larval development in invertebrates and discussed the ecological advantages and disadvantages of each type, but did not dwell on their evolutionary significance. The solitary capitate is seldom very small because it has to be of moderate size to carry out all its functions of nutrition and reproduction. The large yolky eggs of some Tubularians may only reflect the minimum size at which such a polyp can become self supporting and at the same time be a miniature of the adult.¹ With the progressive development of a colonial habit, the primary nutritive polyp can become functional at a much smaller size, permitting a smaller egg size, and an increased reproductive potential, together with greater possibilities for dispersal of young.

(b) *Encystment in Cnidaria*

As mentioned earlier (p. 480) it is only recently that it has become known that prolonged encystment of the fertilized egg takes place in any Capitate hydroid. As this phenomenon may have some bearing on the evolution of the attached, bottom dwelling hydroids, I propose to discuss it briefly from a wider viewpoint than covered by the title of this paper.

It has already been noted that the autumnal eggs of the pelagic tubularian

¹ Dr. Bertil Swedmark has kindly pointed out that egg-sizes in the minute Cnidaria of the sand fauna bear no relation to the figures given here for the macroscopic forms.

Margelopsis haeckeli are larger than the summer eggs (Werner, 1955). Unlike the latter, they do not develop immediately into young hydranths, but form plano-convex cysts on the substratum and persist in this condition throughout the winter, giving rise in the spring to young pelagic hydranths (Text-fig. 31). This explains

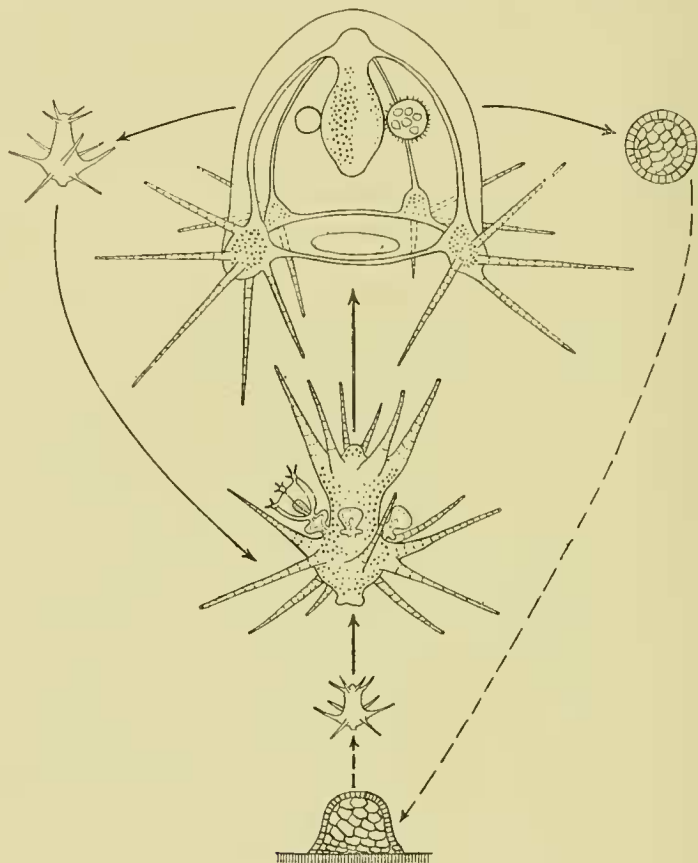


FIG. 31. The life cycle of *Margelopsis haeckeli* Hartlaub: summer eggs are small and develop into actinulae while the larger autumnal eggs pass through a winter resting stage (redrawn from Werner, 1955).

the sudden seasonal appearance of the hydroids and their medusae in the plankton of the southern North Sea for a short period in July and August. Here encystment for a considerable period of the year appears to be an essential part of the life cycle.

We do not know whether a cyst is formed by the primitive capitate hydroid *Tricyclusa singularis* (Schulze). In this species the hydroid suddenly appears in May-June and in some years becomes exceedingly abundant by asexual budding.

Then in July it develops fixed gonophores and by August has disappeared again until the following year. This seasonal appearance and the plano-convex form of the basal disk by which it is attached to the algal substratum suggests that it has an encysted winter stage, and that it may retain this disk as a means of attaching itself to the substratum without the aid of anchoring filaments (see Text-fig. 6 page 462).

Similar plano-convex cysts are formed by the hydroid of the limnomedusa *Ostroumovia inkermanika* according to Kramp and Paspaleff (1938, p. 35, figs. 10 and 11). It will have been noted (p. 480) that the newly fertilized eggs of *Corymorpha* are covered with a thin layer of perisarc, a condition normally associated with encystment, but here the young hydroid develops (at least in the laboratory) without any delay.

In the scyphomedusan genus *Cyanea* (as in many hydroids without lecithotrophic eggs) the fertilized egg develops into a planula first and encystment is rather variable. Hargitt and Hargitt (1910) in discussing the development of *Cyanea arctica* (regarded as a form of *C. capillata*) think that the encystment of the planula "is a condition often common where development is limited to the laboratory." They add: "whether such a condition ever occurs in nature we have no means of knowing, but so far as recalled it has not been made a matter of record. All observations point to the conclusion that the phenomena associated with encystment are expressions of adaptation due to unfavourable conditions of environment". They note that McMurrich (1891) and Hyde (1894) differ about this.

McMurrich's account indicates that the majority of his planulae encysted, forming the typical plano-convex type of cyst, but that a few developed without becoming attached and without secreting a plano-convex cyst. My own observations (on *Cyanea lamarchi* Péron and Lesueur) agree with his in that "every young Scyphistoma was attached to a cyst, its stalk passing through the opening and spreading out on the lower flat wall." Hyde, on the other hand, noted encystment only in one embryo.

It is noteworthy that the Hargitts found that metamorphosis from planulae to scyphistomae after attachment took between 20 and 60 days, while some had not developed at the end of the period. They give figures of young scyphistomae suspended from their empty cysts, the latter acting as floats (Hargitt and Hargitt, 1910, figs. 38-41).

McMurrich stated that the encysted stage lasted for several days, while in my own experiments the young scyphistomae developed within 48 hours of settlement of the planulae.

Encystment in other Scyphozoa had been noted earlier by Kowalevsky (1884) in *Lucernaria*. The presence of a basal disk in *Stephanoscyphus*, the polyp-like scyphistoma of the Coronatae, also suggests that a cyst is formed here. The sum of these notes indicates that encystment is common to the Anthomedusae and the Limnomedusae in the Hydrozoa and to the Stauromedusae, the Coronatae and the Semaestomeae in the Scyphozoa, although its occurrence has been noted in very few species.

It is of course well known that the egg may encyst in various species of *Hydra*, but encystment here may possibly have arisen in response to the need for such a device in fresh water where ponds are liable to dry up periodically.

We do not know enough about encystment in the Hydrozoa and Scyphozoa to assess its full significance but as already suggested the occurrence of the plano-convex cyst in widely divergent groups all exhibiting some kind of alternation of generations, may have a bearing on the evolution of the hydroid phase. Its elaboration from a resting stage, at first merely developing directly into a medusa, then gradually acquiring a polypoid form and budding daughter medusae, and evolving to a feeding polyp with tentacles can be readily envisaged, but is less attractive than the actinula theory for which there is more supporting evidence (but see p. 503).

5. THE DEVELOPMENT OF PERISARC

Before considering the development of the perisarc proper it may be appropriate to consider the phenomenon of the secretion of a thin pellicel by the fertilized egg in *Corymorpha*. This has been noted in *Corymorpha palma* (Torrey, 1907) and in *Corymorpha nutans* (Rees, 1937a) and seems to be the last surviving indication that encystment was a regular feature in the ancestral Corymorphines, but it has disappeared completely in species like *Tubularia* in which the egg develops directly into an actinula on the manubrium of the sporosac.

The way in which the eggs of *Corymorpha* attach themselves to the substratum is also significant. In *Corymorpha nutans*, "The pellicel of the egg is very elastic and is pushed out into broad pseudopodia-like growths on the underside into contact with the substratum to which the pellicel adheres. The so-called 'pseudopodia' then withdraw into the main body and the dilated pellicel shrivels up into a small tube. Several of these may be formed (Text-fig. 32) and they anchor the egg to the substratum. They may be termed anchoring filaments. The young developed

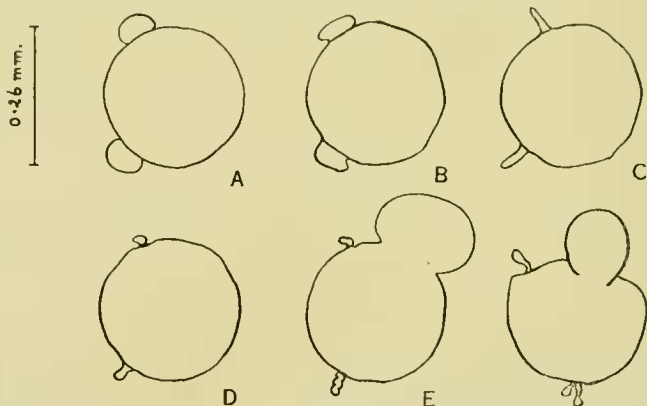


FIG. 32. *Corymorpha nutans* M. Sars: successive movements during the attachment of the pellicel of the egg to the substratum by anchoring processes (after Rees, 1937a).

directly out of the eggs into young polyps" (Rees, 1937*a*, pp. 743-744). In *C. palma*, however, Torrey notes that after hatching out the larva wanders about before settling. In both species it will be noted that the period of encystment is very brief and that the pellicel is very thin. What is of great interest however is the mode of anchoring the egg which is analogous to the development of filaments for anchoring in the mud living polyps of *Corymorpha*, *Euphysa*, *Hypolytus*, *Acaulis* and some species of *Myriothele*.

In the evolution of the hydroid phase culminating in the complex Sertulariidae and Plumulariidae, with the total suppression of the medusa phase, we see a gradual increase in the complexity of the perisarc; this becoming very important as an elaborate framework for the arrangement of the hydranths.

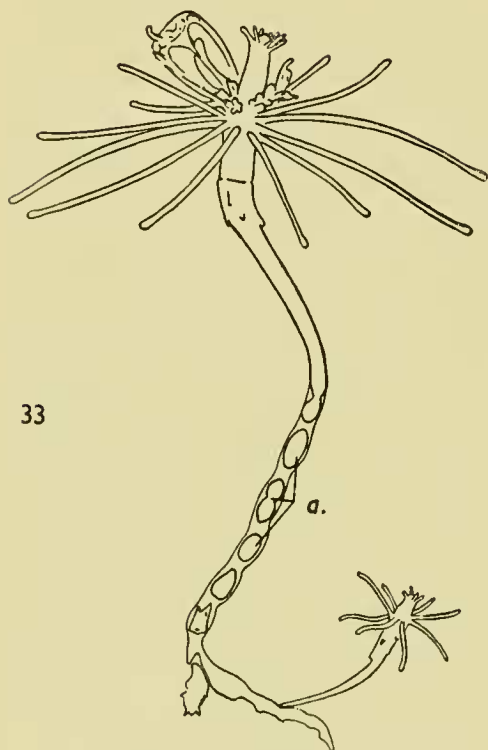
In the solitary hydroids the perisarc is either feebly developed or remains fairly simple. I am inclined to believe that the most primitive hydroids had little or no perisarc and in the simpler forms we have a condition approaching this in the lower Corymorphines and in *Tricyclusa*.

Mud-living forms like *Euphysa*, *Hypolytus*, *Amalthaea*, and *Acaulis* have a feebly developed, poorly chitinized perisarc which forms a loose sheath around the stem of the polyp. It is a rather gelatinous structure, to which mud particles adhere, and can be discarded if necessary, and a new one secreted by the polyp. *Corymorpha nutans*, which lives on firmer sandy or sandy-mud substrata, has a more closely-adherent perisarcal sheath. Associated with this rudimentary tube are a number of filaments which are used for anchoring the polyp; they are also covered with perisarc and their tips become attached to grains of sand or other firm particles, so anchoring the organism. Typically they form a basal tuft at the base of the stem.

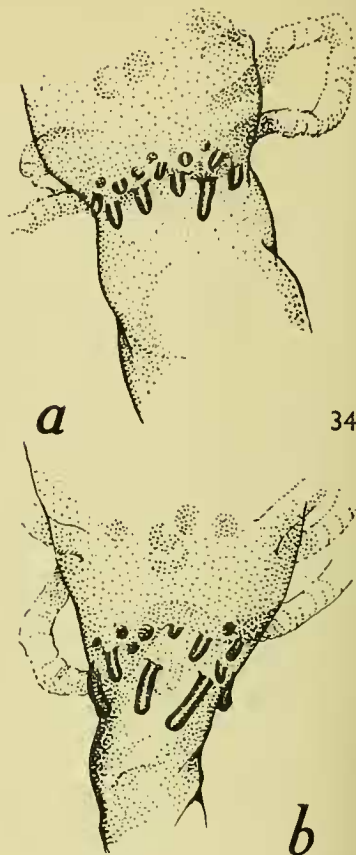
In the lower Corymorphines, such as *Hypolytus* and *Euphysa*, the filaments are quite few. Here the stem is known to become constricted off into a number of asexual bodies, sometimes leaving only the hydranth when the process is completed (Text-fig. 33). In these polyps the rudiments of filaments are always found in a ring around the posterior border of the hydranth below the aboral tentacles (Text-fig. 34). This may be the ancestral position of the filaments and it appears that these lie near a zone of growth, and so with the development of a new stem, are carried away from the hydranth proper.

To return for a moment to the actinula, it is possible to imagine an ancestral form, drifting over the sea bottom, anchoring itself by aboral processes, these evolving into the well known anchoring filaments (analogous to those of the eggs of *Corymorpha*). The position of these processes on the hydranth in the primitive Corymorphines suggests that they may have arisen by modification of some of the tentacles of the actinula. However, whatever their origin, the anchoring filaments and the loose, semi-gelatinous sheath, are primitive features found only in solitary hydroids.

The full development of anchoring filaments is best seen in the higher Corymorphines, where, in *C. nutans* and related forms, there is an enormous tuft at the base of the stem; this firmly anchors the polyp in sand or sandy mud and represents the highest development of this mode of anchoring. Occasionally too, the filaments



33



34

FIG. 33. *Euphysa farcta* (Miles): a simple Corymorphine in which the stem becomes constricted off into a number of asexual bodies (redrawn after Miles, 1937): a., asexual bodies.

FIG. 34. *Euphysa aurata* Forbes: posterior border of hydranth with rudiments of filaments, A, Trondheimfjord (Fillan-fil-fjord, between Hitteren and Fjeldväröy), dredged 150 m., 21. viii. 1937; B., Trondheimfjord (Strindfjord), dredged 90 m., 21. viii. 1937: both collected by Dr. Jöran Hult.

can give rise to young polyps (Text-fig. 35) which become cut off during their growth from the parent. This may perhaps be a reminder of the way in which some simpler ancestor developed stolons and so gave rise to the colonial Corynidae and their allies.

In *Acaulis primarius* the gelatinous tube and the filaments are retained but in several species of *Myriothela* including the northern *Myriothela phrygia* (Fabricius), the tube is lost and only the filaments are left for anchoring (Text-fig. 36). These are chitinized and their mode of attachment has been described by Manton (1940

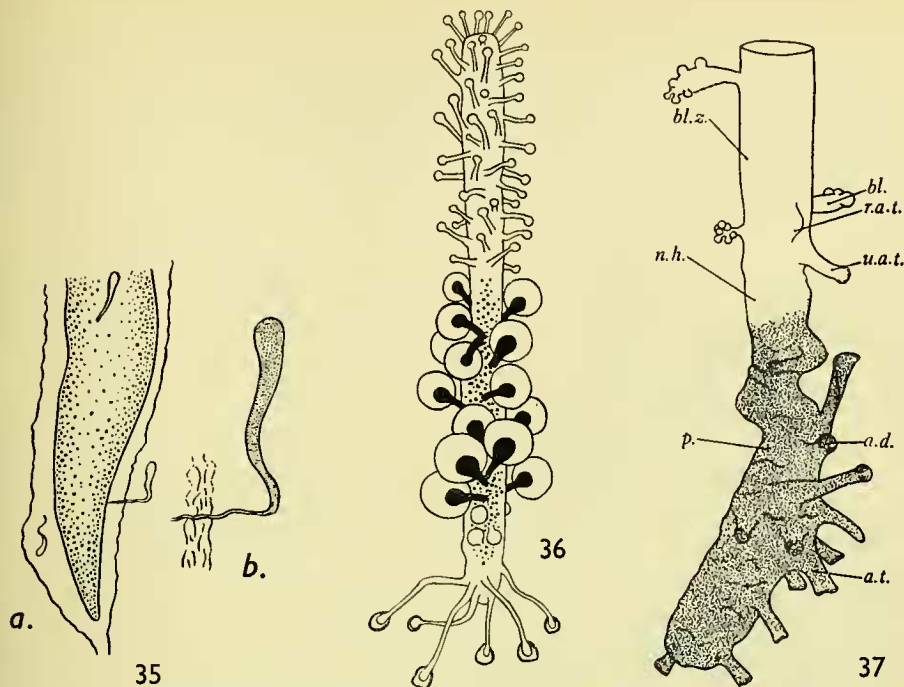


FIG. 35. Young polyp beginning to differentiate from a frustule in *Corymorpha nutans*; from a specimen in Zoologiske Museum Copenhagen (taken at Frederikshavn, 27th July, 1931).

FIG. 36. *Myriothele phrygia* (Fabricius): note the naked polyp with perisarc only on the dilated ends of the anchoring filaments (redrawn from Sars, 1877); for the sake of clarity only half the capitate tentacles have been shown.

FIG. 37. *Arum cocksi* Vigurs: lamellar basal perisarc with modified anchoring filaments (after Manton, 1941).

and 1941) in detail. Had Manton been familiar with those of *Corymorpha* she would have recognised that her description of the "adhesive tentacles" of *Myriothele phrygia* in the following terms: "many of them appear to have shrunk in diameter, so leaving the terminal disk of the attachment appearing much wider than the stem" applied also to the filaments of *Corymorpha*. There is no doubt that they are homologous.

Arum cocksi presents an interesting transitional stage as regards perisarc between the filament type of anchoring and the development of a firm adherent perisarc. In this species the basal portion of the hydranth is covered by perisarc, which according to Manton (1941) is roughly cylindrical in shape, but distorted to fit irregularities of the substratum (Text-fig. 37). Here the anchoring filaments are short, finger-like projections from the surface of the perisarc sheath (the

hydrorhiza of Manton) with flattened disk-shaped ends which adhere to the substratum in the manner described by Manton, that is, "the chitin forming a disk of adhesion is thick, and is attached to the mesogloea of the tentacle". Some evidence is put forward by Manton which suggests that in *Obelia*, for instance, the mode of attachment of the stolons is different and that no mesogloea is involved, but for the simpler capitate forms we have no evidence of what happens.

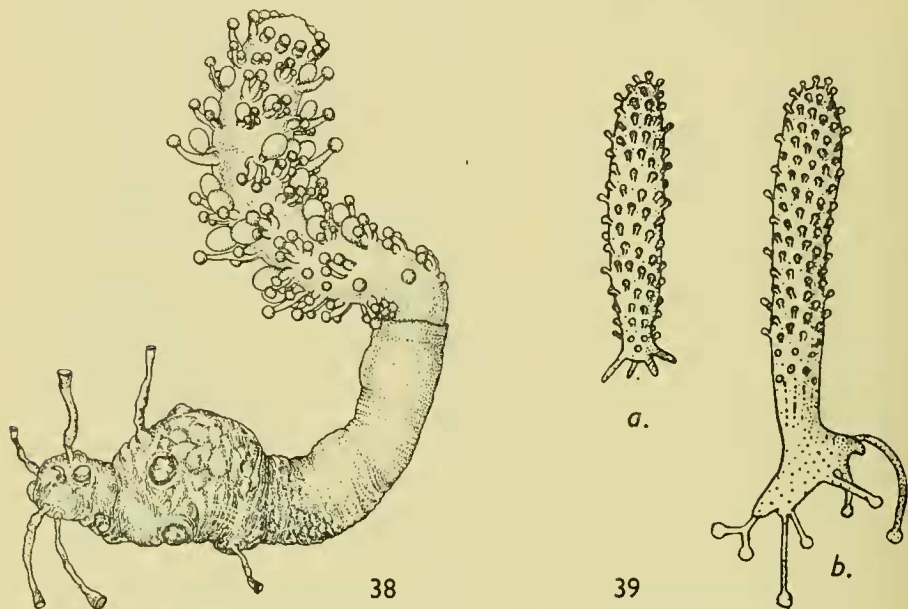


FIG. 38. *Monocoryne gigantea* (Bonnievie): sketch of a syntype from Hammerfest in the Zoologisk Museum, Oslo. Note the tubular basal perisarc and the few stout anchoring filaments.

FIG. 39 A and B. *Arum cocksii* Vigurs: regeneration and attachment to substratum by means of anchoring filaments (after Billard, 1921).

Here may also be mentioned *Monocoryne gigantea* (Bonnievie), a rather aberrant species, which, while having some obvious affinities with *Myriothele*, stands rather on its own in the *Acaulis-Myriothele* group of hydroids. As regards development of perisarc it shows an interesting transitional stage, the lower part of the polyp being clothed in a sheath of perisarc, which is much firmer and more closely adherent to the polyp itself than in *Acaulis* and has a few strong filaments at the base for attachment (Text-fig. 38). These features were noted during a re-examination of Bonnievie's two specimens in the Zoologiske Museum, Oslo in 1955. I was not able to ascertain whether any of the basal perisarc of the polyp itself could be termed adherent.

Regeneration and the re-attachment of the cut stem of *Arum cocksii* by means

of filaments (Text-fig. 39) without the preliminary formation of a basal sheath has been described by Billard (1921). In this species the proximal end of the mutilated polyp puts out several processes which attached themselves to the substratum just as the filaments of *Corymorpha* do. In the higher Filifera, in *Amphinema dinema*, for example, the settling planula almost invariably puts out a three-rayed stolon to fix itself on the bottom and I am inclined to regard these rays as homologous with anchoring filaments—the latter being primitive and to be regarded as forerunners of true stolons.

Tricyclusa singularis, as an unique survivor of an aberrant group of early capitate hydroids, has a very interesting kind of perisarc. The hydroid is solitary and is attached to the surface of seaweeds and *Zostera* by a pedal disk, comparable to what is found in the hydroid of the Limnomedusa *Ostroumovia* and in young scyphomedusan scyphistomae. Distally this expands into a dilated, poorly-chitinized sheath into which the hydranth is partially retractile. The gelatinous sheaths in *Euphysa*, *Corymorpha* and *Tricyclusa* are clearly homologous because all three genera are obviously derived from the same early Corymorphine ancestors (but see p. 514).

It is only in these aberrant survivals that we see nature's experiments in the direction of a firm perisarc, but this essential step preceding the development of a colonial habit must have taken place in a comparatively unspecialized Corymorphine ancestor, in which the capitate oral tentacles were retained and in which the aboral whorl had already become filiform. The larva of *Corymorpha nutans* is rather like this and except in its stem and mode of anchoring is rather similar to young polyps of colonial corynid hydroids like *Stauridiosarsia* and *Cladonema*.

This evolution of firm perisarc probably accompanied the change from a soft mud or sandy habitat to a firm substratum and meant the disappearance of the typical filament, or it might be said that the filament became transformed into a permanent structure, the creeping stolon, attached along its entire length to the substratum. This enabled a firm perisarc to be evolved, and this in turn, provided the secure holdfast required for elaboration into a colony with polyps at intervals along the stolon. The evolution of firm perisarc, too, meant that it could acquire definite shape, such as ringing and internodes. These in turn depend on the way growth takes place as indicated by Berrill (1952) in the following terms: "Growth occurs rhythmically, or in pulses, which when in slow succession becomes recorded by the polymerizing perisarcular chitin as annuli. When occurring in rapid succession, the perisarcular annuli have no time to form, and straight perisarc results. The alternation of annular and internodal perisarc is indicative of a major rhythm of growth superimposed on the basic pulsation."

6. THE MEDUSA OF CAPITATE HYDROIDS

In this group (the Codonidae of Haeckel) it is generally agreed that the medusa is among the simplest in the hydromedusae, although it must be admitted that there are also some highly specialized and rather aberrant forms especially in the Cladonemidae and Eleutheriidae.

The ancestral Codonid can be envisaged as having a deep bell-shaped umbrella with nematocysts, either scattered over the exumbrella, or arranged in perradial tracks (Text-fig. 40). The stomach would be tubular with a simple circular mouth and the gonad would completely encircle the stomach. Four radial canals, a ring canal and four perradial tentacles complete the picture of the ancestral codonid and few would disagree with this interpretation. To this, I would add that the tentacles were probably moniliform and it is possible that budding of daughter

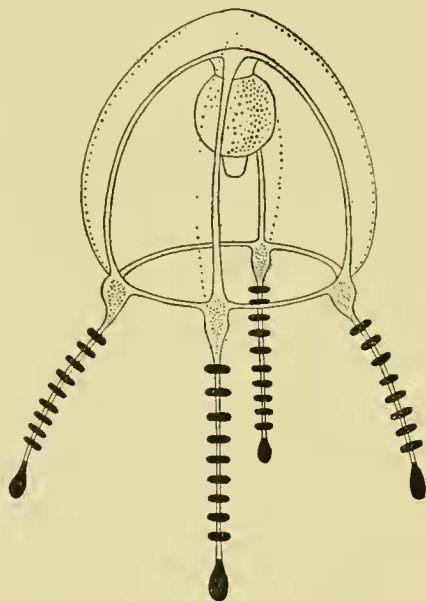


FIG. 40. Diagrammatic representation of an ancestral Codonid medusa with ring gonad, exumbrellar nematocyst tracks and four perradial tentacles with moniliform arrangement of nematocyst batteries.

medusae from the stomach would take place before maturation of the gonads. Medusae of the genus *Sarsia* are recognized as departing but little from the generally accepted idea of a simple codonid but two features require comment.

The more usual arrangement of nematocysts on the exumbrella is the scattered one, but there are some nematocyst tracks in various forms, *Ectopleura* (Text-fig. 41) and *Hybocodon* (Text-fig. 42) in the Tubulariidae, *Neoturris* in the Pandeidae, and special tracks in *Zanclea* and various "pteronemids" and *Proboscidactyla stellata* (Limnomedusae);¹ all are widely divergent forms and this may imply the persistence of an ancestral character (see p. 504).

¹ The type of nematocyst track found in *Zanclea* is also found in the *Chrysomitra* medusae of the Chondrophora which are believed to have a Capitate ancestry (Totton, 1954; Picard, 1955).

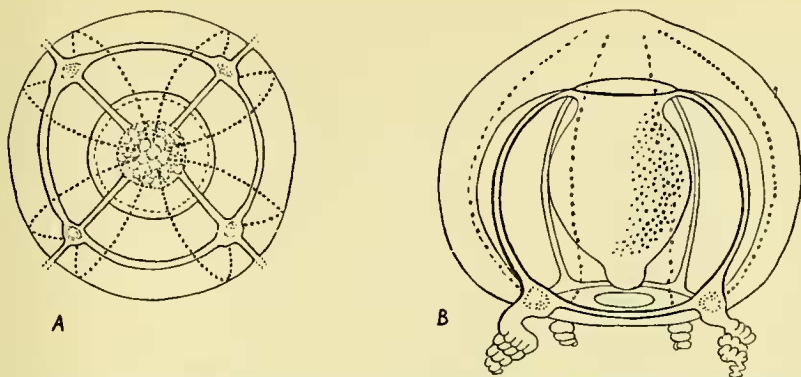


FIG. 41. *Ectopleura dumortieri* (van Beneden) : A, apical view of medusa with 8 nematocyst tracks ; B, side view of medusa (redrawn after Russell, 1953).

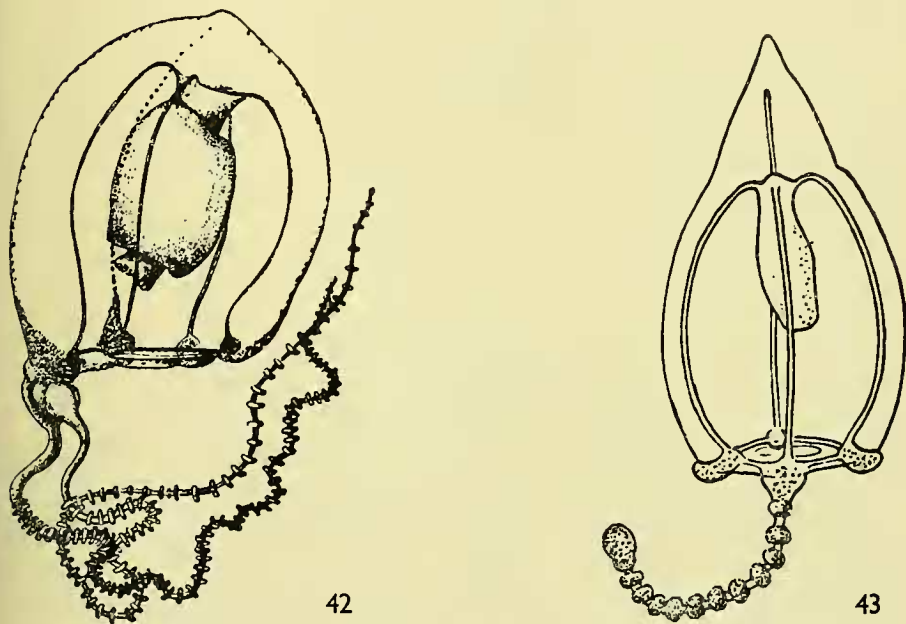


FIG. 42. *Hybocodon prolifer* L. Agassiz : medusa (after Hartlaub, 1907). Note the exumbrellar tracks and the moniliform arrangement of nematocysts on the tentacles.

FIG. 43. *Corymorpha nutans* M. Sars : young medusa with partially extended tentacle (after Russell, 1953).

There is much evidence for regarding the moniliform arrangement of the nematocyst batteries on the medusa tentacle as a primitive character. This arrangement is retained in its most perfect form in *Corymorpha*, (Text-fig. 43) *Euphysa* (Text-fig. 44) and *Hybocodon*, but as already noted it is only in *Euphysa*¹ that this condition exists in both hydroid and medusa (Text-fig. 5, page 460). This type of tentacle is found in other families of the Capitata in a reduced or modified form, but in the Filifera with further reduction and scattering of the nematocysts, traces of the original moniliform arrangement are lost.

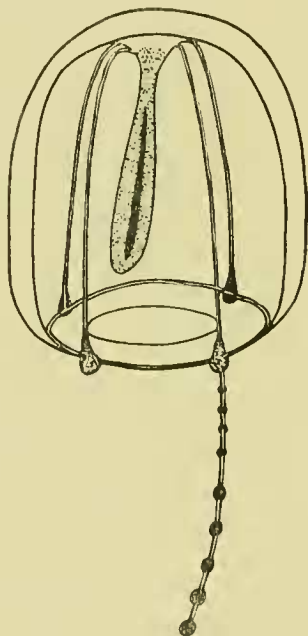


FIG. 44. *Euphysa aurata* Forbes: newly liberated medusa with extended moniliform tentacle (after Hult, 1941).

Even in the Tubulariidae this arrangement becomes modified in *Ectopleura dumortieri*, and in *Gotoea typica* the armature becomes reduced to a single terminal knob. It is in the Corynidae that the reduction is best seen in *Sarsia eximia*, *Dipurena halterata*, *Dipurena ophiogaster* and in *Sarsia prolifera*. In *Dipurena strangulata* (McCrary) there is only a single terminal knob. (Text-fig. 45).

There is doubt whether the grouping of nematocysts into half rings or spiral clasps in many Limnomedusae arose from the moniliform arrangement; there is however a tendency for them to be moniliform in the hydroid *Annulella gemmata* (Ritchie, 1915) and in the medusa *Gonionemus vertens* (Russell, 1953, p. 400, fig. 263).

¹ *Mocrisia* and other related forms are excluded from discussion in this paper for their status requires elucidation.

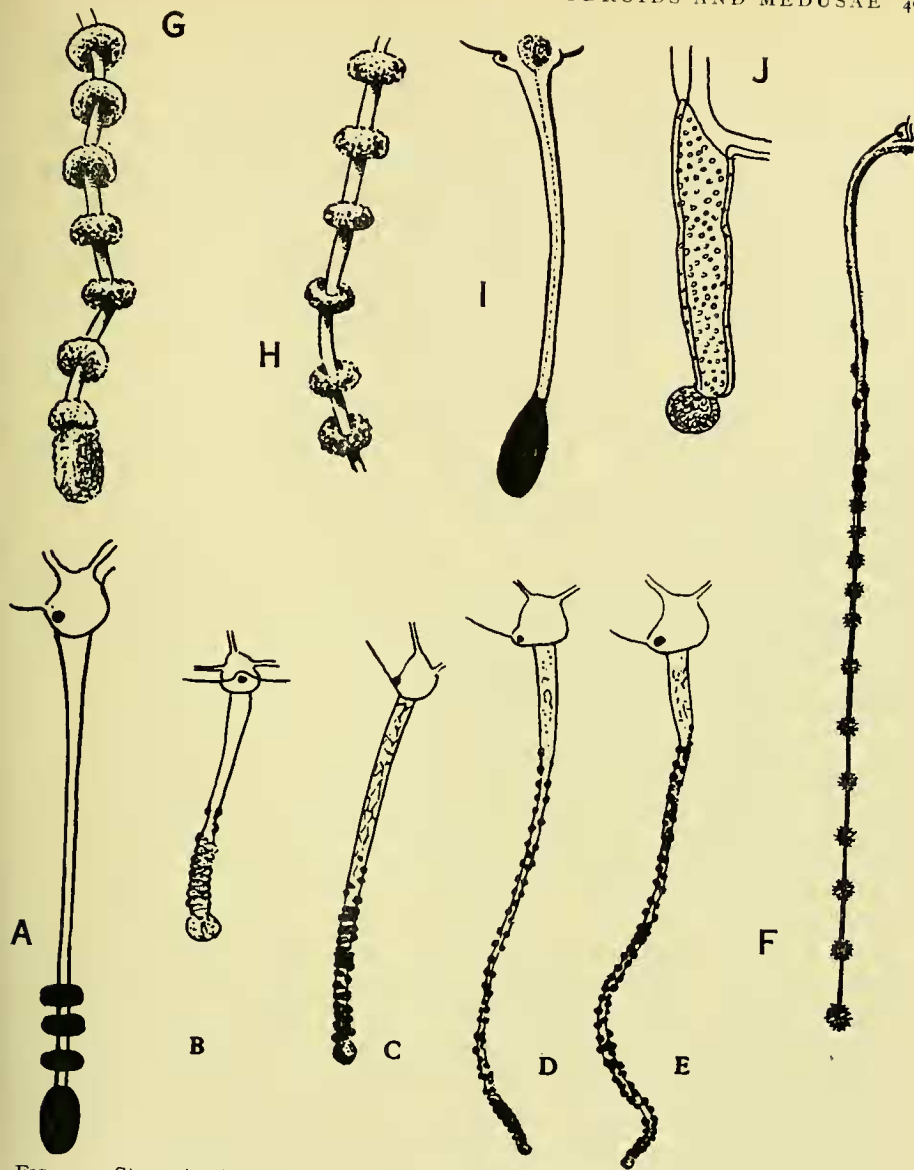


FIG. 45. Stages in the reduction of the moniliform tentacle in capitate medusae: A, *Dipurena halterata* (Forbes); B and C, *Sarsia gemmifera* Forbes; D, *Sarsia prolifera* Forbes; E, *Dipurena ophiogaster* Haeckel; F, *Sarsia tubulosa* (M. Sars), juvenile; G, *Corymorpha nutans* M. Sars; H, *Euphysa aurata* Forbes; I, *Dipurena strangulata* McCrady; J, *Gotoea typica* Uchida: A and I, (original); B-E, G and H, (after Russell, 1953); F, (after Allman, 1872); J, (after Uchida 1927).

It has always been recognized that the aboral tentacles of the tubularian actinula can be homologized with the marginal tentacles of the medusa. It follows that the stomach of an Anthomedusan (where budding takes place and the gonads develop) corresponds to the region immediately anterior to aboral tentacles in the hydroid—and this is the region where these activities take place in the Capitata in general.

Budding of daughter medusae from the manubrium is the more common method seen in Anthomedusae (e.g., *Eucodonium brownei* and *Sarsia gemmifera* in the Capitata, and *Lizzia blondina* and *Rathkea octopunctata* in the Filifera). Less commonly there may be budding from tentacle bulbs on the bell margin (as in *Hybocodon prolifer* and *Sarsia prolifera*). This seems to be a less primitive site for budding than the manubrium. In the latter ingested food is absorbed and made immediately available on the spot for building up the tissues in budding; there are no transport problems as in *Sarsia prolifera* where food has to be carried along the radial canals to the tentacle bulbs for use there. In this respect perhaps *S. prolifera* may have evolved a more efficient means of dispersing food along its radial canals thus enabling it to produce medusa buds at some distance from the point of ingestion and its swimming movements are unhampered by having the subumbrella cavity filled with young buds.

The evolutionary significance of the development of an efficient means of dispersing food in the hydroid is discussed on p. 477.

The mouth is simple without armed lips or oral tentacles in most Codonid medusae and this is generally regarded as the primitive condition. In the hydroid of the Tubularians (Tubulariidae and Corymorphidae) the oral whorl appears late in the development of the actinula and must be regarded as a secondary character evolved in the primitive Corymorphine hydroids.

In the higher Anthomedusae the mouth of the medusa may become armed in various ways. This may take the form of lips armed with nematocyst clusters as in *Cladonema* (Plate 13, figs. 7 and 8) and the Hydractiniidae, or the lips may become frilled and armed with a continuous band of nematocysts along their free margin as in *Turritopsis* or there may even be simple or branched tentacles situated close to the mouth as in *Bougainvillia*.

Branching in the medusa tentacle is found in the Cladonemidae and the Eleutheriidae; in the latter the tentacle bifurcates, the one branch carrying an adhesive organ and the other a nematocyst cluster at its tip. In *Cladonema* however, the tentacle is branched and part of it may be said to be coryniform just as in the tentacles of the hydroid *Cladocoryne* (Text-fig. 54, page 511) and the blastostyles of the hydroid *Arum cocksii*. The appearance of this type of tentacle in *Cladocoryne* and *Arum* is a feature which provides a link between these two forms but it is not sufficient evidence to prove that *Cladocoryne* has an Acauloid ancestry. This tentacle, in the *Cladonema* medusae, seems to have arisen independently for the *Cladonema* hydroid cannot be derived from a myriothelid stock.

Mention must also be made of two other features of specialized medusae. There is a tendency in the Filifera for the gonads on the manubrium to become split up. In the Capitata this condition is found in *Gotoea typica* (tentatively placed in the

Tubulariidae by Uchida) and in *Zanclea* where the gonads are split into four inter-radial groups. In *Eleutheria*, to quote Mayer (1910, p. 93), "There is a peculiar brood pouch above the stomach but this pouch is not connected with the gastrovascular cavity of the medusa. The cavity of this brood pouch is, however, connected with the bell cavity by means of simple, interradial openings. The products are developed exclusively in the epithelial lining of this brood pouch, which is derived from the ectoderm of the subumbrellar cavity of the bell". (Text-fig. 48, page 500).

Eleutheria is of course highly modified for an ambulatory existence on seaweeds but similar brood pouches have been described in *Pteronema*, *Ctenaria* and *Dendronema*.

7. THE VALUE OF THE GONOPHORE IN CLASSIFICATION

Widely divergent opinions have been held about the value of the gonophores in the classification of this group, and much of the confusion in classification at generic level is due to the lack of unanimity on this score. Early authors notably Allman (1864) laid particular stress on whether the gonophore became free, as a medusa, or remained fixed, as in a sporosac, and this is broadly also the view of Stechow (1919, 1923). Allman even goes further in saying "each of these forms of gonophore may itself present differences which will afford characters of value in the limitation of our genera". This implies, and was often subsequently interpreted as meaning, that differences in the degree of reduction of the gonophore (eumedusoid, crypto-medusoid, heteromedusoid and styloid kinds) could be used to distinguish genera (Text-fig. 46). These types of gonophore were regarded as important in the definition of genera by Kühn, but he was not always consistent, for he used them as specific characters in the genera *Podocoryne* and *Hydractinia* (1913, p. 227).

At the other extreme, Levinsen (1893) believed that no generic distinction should be drawn between hydroids that were co-generic on hydroid characteristics, even if some gave rise to free medusae and others to fixed gonophores. Indeed there is much to commend this approach to the specialist who only knows his species as something dead in a bottle.

It is to Broch (1915, 1916) that we owe the most lucid account of the bearing of the gonophores on classification. He demonstrated very clearly that the degree of reduction of the gonophore was most unsuitable as a generic character because of sexual dimorphism, for he was able to show that the male gonophores might be more reduced than the female ones, as in some species of *Tubularia* (Table III).

Broch was also concerned with the status of genera like *Coryne* and *Syncoryne*, *Hydractinia* and *Podocoryne*, where the sole criterion is assigning species to one or the other is whether they have fixed or free gonophores. Following Levinsen he merges the genera, as does Kramp (1935a) for *Corydendrium*. Kramp (1949) supports Levinsen's views in the following terms: "I wish to state that the degree of development or reduction of the gonophores is not a generic character" and adds that a line should not be drawn between two groups of species merely on account of

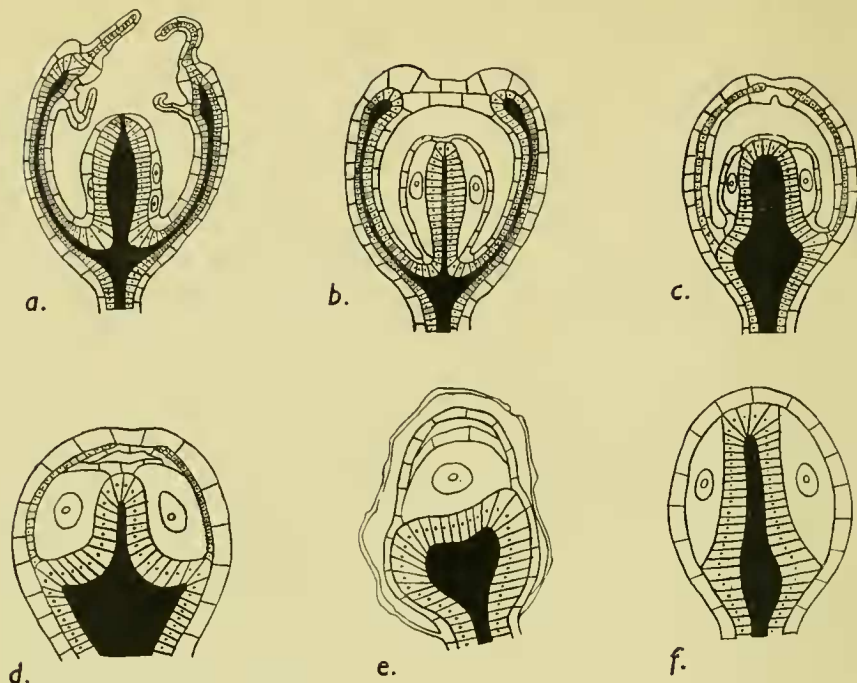


FIG. 46. Diagrammatic longitudinal section of the different stages in the reduction of the gonophore: A, medusa; B, eumedusoid; C and D, cryptomedusoid; E, heteromedusoid; F, styloid (redrawn from Kühn, 1913).

TABLE III.—Degree of Reduction of the Gonophores

	Medusa.	Eumedusoid.	Crypto-medusoid.	Styloid.
<i>Corymorpha nutans</i> M. Sars . . .	×
<i>Corymorpha glacialis</i> G. O. Sars	♂ + ♀
<i>Corymorpha groenlandica</i> Allman	♂ + ♀	..
<i>Tubularia indivisa</i> L.	♀	♂	..
<i>Tubularia larynx</i> Ellis & Solander	♂ + ♀
<i>Tubularia regalis</i> Boeck	♀	♂	..
<i>Ectopleura dumortieri</i> (van Beneden) . .	×
<i>Hybocodon prolifer</i> L. Agassiz	×

the gonophores being developed into free-swimming medusae or remaining in connection with the hydroid polyp (the trophosome) as fixed gonophores if no other structural differences imply a generic separation". This scheme works very well and is indeed admirable if each group of species fell naturally into one type of hydroid and one type of free medusa. There are, however, serious difficulties which

make it unworkable in many families. Let us first consider the simple examples shown in Table III of *Tubularia*, *Ectopleura* and *Hybocodon*, where the second and third genera have free medusae each entitled on its own characteristics to generic rank. The *Hybocodon* hydroid is a little less like *Tubularia* than that of *Ectopleura* so that presumably *Ectopleura* could be merged with *Tubularia* although there is no absolute certainty that Tubularian gonophores have been derived by reduction from *Ectopleura* medusae.

As Kramp states: "The medusae *Sarsia*, *Dipurena*, *Linvillea* and *Zanclea* all have polyps resembling *Coryne*, and among the Pandeidae the medusoid genera *Amphinema*, *Halitholus* and *Leuckartiara* all have very similar hydroids. Moreover, the hydroids of these Pandeidae are very similar to those of *Bougainvillia*, though the medusae belong to two different families". In all these groups the problem is the same for we must recognize that the generic differences established for the medusae are sound ones, and in this connexion I cannot agree with Broch (1916) who is disinclined to pay much attention to the free medusae in the classification of hydroids, "On account of their dependence on the outward conditions and their power of plastic accommodation to biological influences, the gonophores are unsuitable for basis of division into genera". But the medusa, evolved as it is for life in a planktonic environment, is an essential part of the organism and leads to a better appreciation of the mosaic representing the whole species.

To return to the problem of the species with fixed gonophores, do we link *Coryne* either with *Sarsia*, *Dipurena* or with *Linvillea* or even found a broad Levinsenian genus which embraces all four genera? Similarly do we unite *Rhizorhagium* with *Bougainvillia* in the *Bougainvilliidae* or with one of the genera *Amphinema*, *Halitholus* or *Leuckartiara* in the Pandeidae. The study of their nematocysts may enable us to ascertain the family status of problem species but so far it shows no great promise for distinguishing genera. Levinsen's theoretical approach cannot be implemented now and there are other considerations which would make any naturalist hesitate to unite genera like *Coryne* and *Sarsia*,¹ even though we have forms like *Coryne lovéni* in which the medusa is fully formed but never released. Each transitional species like this has to be classified on its medusa structure and this species appears to be sufficiently close to *Sarsia* in its morphology to be placed in that genus, and that is where I would classify it. But who knows whether *Coryne pusilla* Gaertner with styloid gonophores is co-generic with it?

Let us consider the free medusa, not as an organ only a little removed from the fixed eumedusoid, but as a living entity.

Once the medusa is released from its hydroid it begins an independent existence which may last for a few hours while it becomes sexually mature (as in *Podocoryne carnea*) or as in the majority of medusae it may live for weeks and even months in the plankton. The typical planktonic medusa may be released at a small size of about 1mm. in bell-height and possess one to four tentacles. It grows by feeding on

¹ *Coryne pusilla* Gaertner is here selected as the type species of *Syncoryna* Ehrenberg, 1834, so that this genus falls into the synonymy of *Coryne* Gaertner. *Sarsia* Lesson, 1843, thus becomes available for both hydroid and medusa of species co-generic with *Sarsia tubulosa* (M. Sars) (the type species of the genus).

the zooplankton and many species have their own fishing technique when using their tentacles for capturing prey. In due course some medusae (according to species) may possess about 150 tentacles and have a bell height greater than 30 mm. but the majority do not attain this size. It may have a characteristic form of gonad, bud daughter medusae, and its eggs may or may not enjoy some measure of brood protection. During all this time too it may exhibit a certain pattern of behaviour and may have its own characteristic kind of diurnal vertical migration.

All these, no less than the morphological structure of the medusa, are essential characteristics of the species, and cannot be divorced from our concept of it.

Enough has been said to demonstrate the wide gulf between the fixed gonophore and the free medusa for me to be in complete agreement with Browne's statement: "I certainly prefer to place Hydroids, like *Bougainvillia*, with planoblasts, and Hydroids, like *Bimeria*, with sporosacs into separate genera, though there may be a few cases in which it is hard to draw the line". (1907, p. 19.)

I had been influenced in some earlier papers by Kramp's arguments in his classification of *Corydendrium* in placing hydroids with fixed and free gonophores in the same genus wherever possible (but I did not subscribe to his views of maintaining separate medusa genera for the medusae of those same hydroids). More experience has convinced me that the classification of hydroids in this way is only feasible in a few well defined groups of species and that the use of separate genera is justifiable and the only suitable course for the vast majority of species in the present state of our knowledge. To avoid any possible misunderstandings, I repeat, that by separate genera, I mean separate genera for hydroids with fixed gonophores and for hydroids with free medusae, the generic name applied to the latter group being used as a common name for the hydroid and medusa of the same species, and not in the sense used by Kramp (1949, p. 188) who puts the hydroid and the medusa of the very same species into separate genera to retain an out-of-date dual classification.

The retention of appropriate genera, in accord with nomenclatorial practice in other groups of animals, for species with or without a pelagic phase will facilitate the creation of a single classification for medusae and hydroids, and at the same time it will be possible to perpetuate old established generic names like *Sarsia*, *Euphysa* and *Podocoryne*, in the medusae and *Coryne*, *Bimeria* and *Garveia* in the hydroids. No insurmountable difficulties will be encountered provided the concept of a type species for each genus is borne in mind. Thus in the Corynidae we have:

Genus.	Type Species.	Type of Gonophore.
<i>Coryne</i> Gaertner, 1774	<i>C. pusilla</i> Gaertner	Fixed gonophore
<i>Sarsia</i> Lesson, 1843	<i>Sarsia tubulosa</i> (M. Sars)	Medusa
<i>Stauridiosarsia</i> Mayer, 1910	<i>Stauridiosarsia producta</i> (Wright)	Medusa
<i>Dipurena</i> McCrady, 1857	<i>Dipurena strangulata</i> McCrady	Medusa

One of Kramp's objections to a single classification for medusae and hydroids concerns the fate of species of which only a part of the life history is known. But their place in any scheme is no different from that of similar species in the present dual

classification, for their status depends solely on whether we consider them co-generic with the type species and the discovery of new facts about them may or may not necessitate minor changes in classification, such as transfer to another genus or even the creation of a new genus for them.

It has already been indicated that on the whole the generic differences established for medusae are sound ones and with minor adjustments can be merged into a single classification for the Athecate or Anthomedusan forms. There is greater diversity of form in the medusa phase and this is not surprising when we consider that the species finds fuller opportunity for expression in a free planktonic phase than in a sedentary benthic phase; the latter often persists in a fairly simple form.

Good examples of this are found in *Cladonema radiatum* and *Dipurena* sp. Vannucci in which the hydroids belong to the basic Corynid type with an oral whorl of capitate tentacles and an aboral whorl of filiform tentacles. In the sterile condition these hydroids are identical in appearance; their medusae however are markedly different, that of *Dipurena* being a typical Sarsiid of the family Corynidae and the other, *C. radiatum*, being so highly evolved and specialized as to require a separate family, the Cladonemidae for it (Plates 12 & 13). Similarly the hydroid *Zanclea costata* (Gegenbaur) could be included in the Corynidae on its trophosome alone but its medusa is a specialized aberrant form also necessitating the status of family rank. (Text-fig. 47).

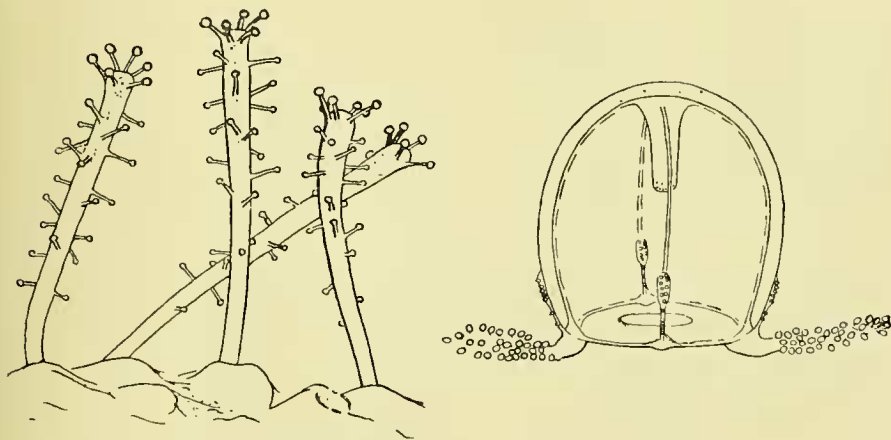


FIG. 47. *Zanclea costata* Gegenbaur: hydroid and medusa (after Russell & Rees, 1936).

Clavatella prolifera Hincks, now more accurately known as *Eleutheria dichotoma* Quatrefages, achieves family rank on the aberrant nature of its crawling medusa but the hydroid looks like a Corynid in which all the tentacles except the oral whorl have disappeared. (Text-fig. 48).

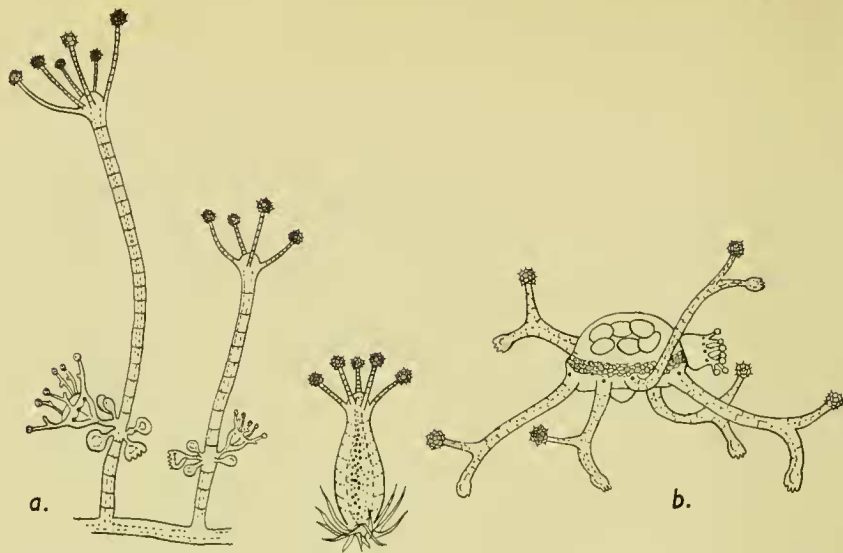


FIG. 48. *Eleutheria dichotoma* Quatrefages: A, hydroid with medusa buds (after Hincks, 1861); B, medusa (redrawn from Russell, 1953).

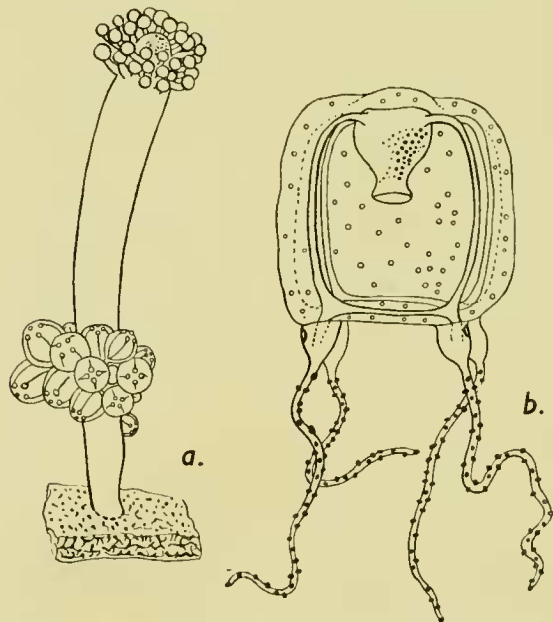


FIG. 49. *Hydrocoryne miurensis* Stechow: A, hydranth with encrusting base (redrawn after Stechow, 1909); B, newly liberated medusa (redrawn from Uchida, 1932).

In *Hydrocoryne* it is the hydroid which has evolved most (Text-fig. 49). The mesogloea has thickened to become the forerunner of a skeletal formation. There is an encrusting base. Here then the hydroid has made considerable progress towards the development of a skeleton but it is noteworthy that its medusa has remained essentially Sarsiid in character. (Text-fig. 49b).

Hydrocoryne and *Eleutheria* have similar polyps in which there is a single whorl of capitate tentacles around the mouth, and, although they appear to have diverged early, seem to have a common ancestor. *Cladonema*, too, seems to have some affinity with *Eleutheria* but here also they have evolved along different lines. The feature of immediate interest is the presence of armed mouth lips in the medusa—this together with the form of the polyp in *Hydrocoryne* and *Eleutheria* suggests that the Hydractiniidae arose from the same common ancestor as these three forms. It should however be noted that no significance is attached to the presence of encrusting bases in both *Hydrocoryne* and *Hydractinia* as these features appear to have arisen in different ways.

In the higher Filifera the hydroid is reduced to the simplest form of nutritive polyp and often the nature of the gonophore is the only means of distinguishing species for certain. Thus in *Stomotoca* (i.e., *Amphinema*) the two British species, almost indistinguishable on trophosome alone, can readily be identified by the newly liberated medusa (Rees and Russell, 1937). Similarly the same holds true for *Bougainvillia ramosa* and *B. superciliaris* hydroids.

The gonophore is thus of paramount importance for recognizing many species and hydroid specialists sometimes commit serious errors in classification through ignoring the diagnostic features of the medusa phase. In this way, Vervoort (1946a) placed *Bimeria* in *Leuckartiara* as a subgenus without realizing that its relationships were with the Bougainvilliidae and not in the Pandeidae where he had assigned it. Consideration of other Bimerid hydroids, which also have the bases of the tentacles of the hydranth clothed in perisarcal tubes (as in *B. vestita*), reveals that they have Thamnostomid medusae and that their real affinities are with the Bougainvilliidae.

There are only a few instances known in which the free medusae are alike and practically indistinguishable and the hydroids are different. The best known example is *Stauridiosarsia producta* whose medusa is indistinguishable from *Sarsia eximia* but differences have been noted in the hydroids. In the *S. producta* hydroid there is a whorl of filiform tentacles and the capitate tentacles have a tendency to be arranged in whorls, while the *S. eximia* hydroid is a typical Corynid. These differences tend to be obliterated however in older colonies of *Stauridiosarsia* for the filiform tentacles may disappear and the capitate tentacles become scattered. There is a suggestion here that we may be dealing with growth stages of the same species, but this requires careful study (see also pages 462-463).

In the Thecata there are no certain means of recognizing the adult medusae of the hydroids described as *Clytia johnstoni*, *C. gracilis* and *C. pelagica* and the medusae now go under the name *Phialidium hemisphaericum* (I.). Similarly it is possible to recognize three forms of *Obelia* hydroid, viz.: *O. geniculata*, *O. dichotoma* and *O.*

longissima but it is not possible to recognize three species of medusa of this genus in the plankton in the areas in which they occur. (Russell, 1953, p. 297).

These few examples however are not typical of the group and in general the medusae are a most useful means of recognizing evolution to specific, generic and even family rank among hydroids which have differentiated but little, or have even become reduced, as regards the trophosome.

8. THEORIES ON THE ORIGIN OF THE ALTERNATION OF GENERATIONS

There are three main theories of the origin of the curious life cycle of hydroids and medusae, viz.: the hydroid theory, the actinula theory and the medusa theory. Of these the second and third are complementary and are the more acceptable to recent workers although the first has some supporters.

1. *The hydroid theory*

For a long time the generally accepted view of the alternation of generations in the Hydrozoa was that the medusa was simply either a reproductive organ or sexual zooid, which, by a process of evolution, had become free for the better dispersal of the reproductive cells (Huxley, 1877). This view that the species was originally represented by the hydroid was also accepted by Gegenbaur (1854, 1878) and Balfour (1880) who thought that the medusa came about by a division of labour and that it was a sexual zooid which had evolved into a free form. They explained the presence of fixed gonophores by assuming that, due to some external causes, some medusae ceased to be liberated and became degenerate. This is broadly also the view of Hamann (1890) who regarded the hydroid as the more primitive and earlier form.

This theory, sometimes called the division of labour theory, was outlined by Leuckart (1851) and elaborated by Grobben (1882). Kramp (1943) states the case as follows: "According to this theory the primary form was a fixed solitary polyp with sexual propagation; it attained the power of vegetative propagation and the formation of colonies, and later on a division of labour was constituted, the power of asexual and sexual propagation being assigned to different individuals; the sexual individuals detached themselves, became free swimming, and were specialized into medusae. According to Grobben the development further proceeded in two different directions: (1) the medusae were reduced to fixed gonophores, as we know them in numerous hydroids; (2) the polypoid form was obliterated, and thus the Trachy and Narcomedusae arose".

Kramp agrees with much of this theory but does not think it can be applied to the Trachylina. He concludes that "the polypoid ancestor of the hydrozoa was first split into a pelagic and a fixed form (I have no opinion as to which of them was the primary form) . . . The Trachylina were developed from the pelagic polypoid progenitor in accordance with the actinula theory (see p. 503); the Leptoliana were derived from the fixed form in accordance with the theory of the division of labour, and thus their special form of metagenesis arose". In his paper Kramp appears to be laying too much stress on the so-called polypoid gonophores of

Corydendrium dispar and on the series of generations which he describes from various hydroid colonies. These "generations" are the logical outcome of the adoption of a colonial habit and the resulting division of labour which set in; they are, of course, descended from fixed polyps but are the latter descended from an actinuloid (Kramp's polypoid ancestor) or was the descent from the actinula of some early medusa? None of the arguments brought forward can dispel the suspicion that the first fixed polyps already possessed a medusa stage; these other views are discussed below.

2. *The actinula theory*

It was Böhm (1878) who first raised doubts about the hydroid origin of the Hydrozoa by demonstrating that there were difficulties in accepting this view, and suggested that a planktonic actinula was the ancestor of both the fixed hydroid and the free swimming medusa. Claus (1880) comes to the conclusion that the hydroid is the larva and the medusa the adult phase and attributes the origin of the hydroid phase to asexual reproduction in the larva.

This view was elaborated by Brooks (1886) who had independently reached the same conclusion as Böhm and Claus from the study of the life cycle of medusae. Böhm thought that the ancestor might be an intermediate form and suggested that the actinula of *Tubularia* might represent the persistent retention of a planktonic ancestral phase. The discovery that the Trachymedusae have a direct development with an actinuloid larva (Metschnikoff, 1874; Brooks, 1886) gave much support to this idea which Brooks elaborated into what he called the actinula theory as follows:

"The view which I believe to be the true one is that the remote ancestor of the hydromedusae was a solitary swimming hydra, or actinula, with no medusa stage, but probably with the power to multiply by budding. I believe that this pelagic animal gradually became more and more highly organized and more perfectly adapted for a swimming life, until it finally became converted into a medusa with a swimming bell and sense organs, developing directly from the egg without alternation, but exhibiting during its growth the stages through which it had passed during its evolution. After this stage of development had been reached, I believe that the larvae derived some advantage from attachment to other bodies, either as a parasite within other medusae, or as what may perhaps be called a semi-parasite, upon other floating bodies such as the fronds of algae; and that it multiplied asexually in this sessile condition, giving rise to other larvae like itself, all of which became medusae."

"I believe that the sessile or attached mode of life of the larvae proved so advantageous to the species, that it was perpetuated by natural selection, and that the primary larva then gradually lost its tendency to become a medusa, but remained a sessile hydra, giving birth by budding to other larvae which became sexual medusae and that the medusa characteristics of these secondary larvae were accelerated, and that the primary larvae gradually acquired, at the same time, the power to produce other larvae which remained permanently, like itself, in the hydra-stage; that in this way the sessile hydra-communities became polymorphic by division of labour,

and that the sessile habit proved so advantageous that the free medusae became degraded into medusa-buds, or sexual buds on the bodies of the sessile hydras or on the blastostyles."

As already mentioned, Claus (1880) came to the conclusion that the hydroid is the larva and that the medusa is the adult and attributes the origin of the hydroid phase to asexual reproduction in the larva.

Kühn (1913) adheres to this idea believing that the ancestral hydroid must have come from a fully developed medusa with a simple hydroid phase, in other words, the kind of life cycle we find in many Trachylina. The simplest trachylines have a direct development (fertilized egg-actinula-medusa), but in some Narcomedusae we find that the actinula larva is parasitic on other medusae and may bud off other larvae, and all (including the original one) develop into medusae. A further advance is seen in *Cunoctantha parasitica* where "the parasitic larva is transformed into a sausage-shaped body, from the surface of which a large number of medusae are developed by budding" (Kramp, 1943, p. 27).

Libbie Hyman (1940, p. 635), too, supports the theory that "the ancestral coelenterate was a primitive medusa" and links this with the actinula theory and it may be added that the two theories are complementary.

As a primitive group of Hydrozoa, the Capitata might be expected to furnish some evidence concerning its origins; this it does to some extent.

The actinula persists in the more primitive families: Tubulariidae (the hydroid *Tubularia*, the medusae of *Ectopleura dumortieri* and *Hybocodon prolifer*), Margelopsidae (the medusae of *Margelopsis haeckeli* and *Climacocodon ikari*) and in the Myriothelidae (in the hydroid *Arum cocksii* Vigurs). (Text-fig. 50). All the above are solitary forms, but an actinula is known in the colonial hydroid *Actigia pusilla* (van Beneden) of the family Corynidae.

There are also polyp or hydranth buds of a distinctly actinuloid appearance in the hydroid *Euphysa aurata*, in *Tricyclusa singularis* and in the hydroid of the medusa *Sarsia tubulosa* (*Coryne sarsii* Lovén) (Text-fig. 51). Mention must also be made of budding from the hydranth in many hydroids of the Order Limnomedusae. Can these polyp-buds also be persistent survivals indicating that the ancestral actinuloid reproduced itself by asexual budding?

There are exumbrellar nematocyst tracks of a simple kind in the medusae *Ectopleura* and *Hybocodon* (in the Capitata) and in a slightly modified form in the Filifera in *Pandea*, *Neoturris* and *Leuckartiara* (Ranson, 1937), and so far as I know no one has commented on their possible origin. It is possible that they arose originally during the development of the medusa direct from an actinula, and that as the metamorphosis took place, some of the nematocysts of the larval tentacles were left behind on the surface as the tentacles grew further and further away from the aboral end of the actinula. On this interpretation then, the perradial nematocyst tracks in Tubularian medusae have persisted from the time their ancestors had a direct development. If we accept the view that the anchoring filaments of the primitive Corymorphine are modified tentacles, this may be regarded as additional evidence in favour of the actinula-medusa theory.

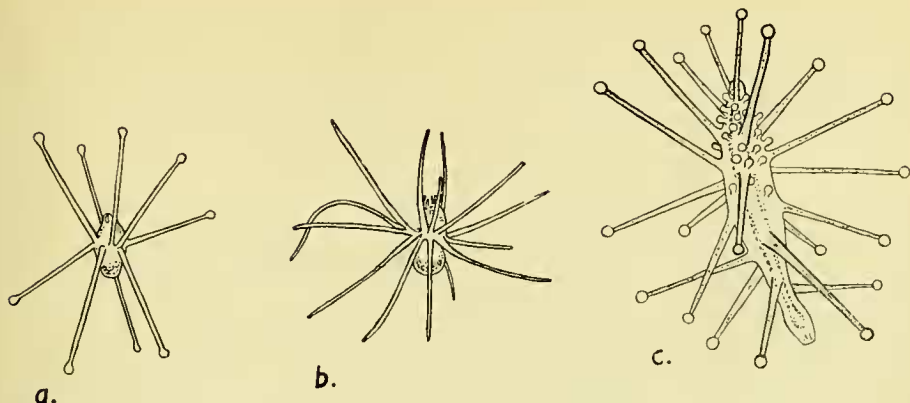


FIG. 50. Actinulae of capitate hydroids. A, *Tubularia* (redrawn from Pyefinch & Downing, 1949), B, *Hybocodon prolifer* (redrawn from Uchida, 1927), c, *Arum cocksii* (Vigurs) (redrawn from Allman, 1875).

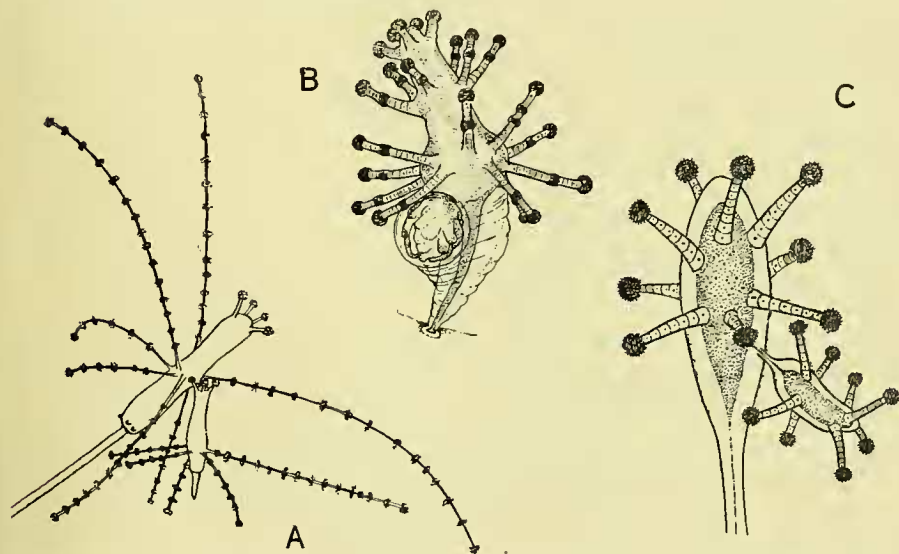


FIG. 51. Polyp-buds in capitate hydroids: A, reversed bud in *Euphysa aurata* (after Rees, 1937b); B, ordinary budding in *Tricychusa singularis* (Schulze) (redrawn from Oppenheim's sketches in the Zoological Museum, Amsterdam)¹, c, polyp budding in the hydroid of *Sarsia tubulosa* (M. Sars) (after Rees, 1941).

As regards the Capitata it is reasonable to assume that their immediate ancestors already possessed a hydroid and a medusa phase, but the actinula-medusa theory harmonizes more closely with what we already know of their origins.

¹ By courtesy of Dr. W. S. S. van der Feen.

In this review the relationships of the Capitata with some members of the Limnomedusae have not been considered for I have no personal experience of working on any of them. It seems however, that forms like *Annulella* and *Ostroumovia* have affinities with the Codonids.

9. MOSAIC PATTERNS AND RELATIONSHIPS

(a) *Mosaic patterns*

As de Beer (1954, p. 10) has stated: "It has long been held by palaeontologists that different parts of organisms are capable of independent evolution, proceeding at different rates". Thus we have in one and the same organism a mosaic of both primitive and specialized characters as demonstrated by Watson (1919 and 1951) in *Seymouria* and *Trimerorhachis* and again by de Beer in *Archaeopteryx*.

In hydroids and medusae I have noticed when considering the sum of the characters of the hydroid and the medusa of the same species that "The result is frequently a mosaic, a blending of characteristics into a pattern which gives a much better picture of the position of the living species than does consideration of only a part of its life history" (Rees, 1956a). In these forms where the two phases of the life history live almost independent existences, it seems easy for them to evolve independently and for each to acquire new characteristics which are not apparent in the morphology of the other.

It is only when we recognize that these hydroids and medusae form mosaic patterns that we begin to have an understanding of possible lines of evolution within the group, and each species has to be assessed not only as I have indicated above, but also against the general picture of evolution in the class as a whole. Only in this way can we reach a rational classification with some relation to phylogeny. There are many excellent examples of mosaic evolution in the Capitata and a brief survey of some key species will help to a better understanding of relationships.

As has been apparent from the earlier part of this paper, I am inclined to the view that the Hydrozoa are medusoid in origin and that the hydroid phase is a later development. Once established however the hydroid phase has become the dominant one to the exclusion of the medusa phase in the most advanced hydroids of the Haleciidae, the Sertulariidae and the Plumulariidae. This trend towards elimination of the medusa phase is apparent however at all levels of hydroid evolution so that even in the most primitive hydroids like *Hypolytus peregrinus* and *Euphysa aurata*, we find that the one has styloid gonophores and the other a free medusa and as regards this particular feature the former may be regarded as the more highly evolved.

The characteristics of the important species in the Capitata have been brought together in the series of mosaic patterns below; they will serve as an introduction to the discussion of relationships which follows.

The first eleven species considered below are solitary forms.

Hypolytus peregrinus Murbach

This is the simplest type of Corymorphic hydroid known to us and is probably

the most primitive of Capitate hydroids (Text-fig. 4). It has two whorls of moniliform tentacles, and a soft, poorly chitinized sheath secured to the bottom by anchoring filaments. This tube can be abandoned and a new one secreted. There is no diaphragm in the hydranth and no canals in the stem. All these are primitive features but the possession of fixed styloid gonophores is a specialized feature.

Euphysa aurata Forbes

This hydroid has the same primitive features found in *Hypolytus peregrinus* but the oral tentacles have become shortened to a single terminal knob (Text-fig. 5).

The medusa has the primitive moniliform tentacle of the same type as is found in the hydroid. The ring gonad and simple mouth are characteristic Codonid features. The medusa is specialized in having lost all but one of the perradial tentacles. It is not certain whether the absence of perradial nematocyst streaks on the exumbrella means that they have been lost (Text-fig. 44, p. 492).

Boreohydra simplex Westblad

This Corymorphine is primitive in the absence of a diaphragm in the hydranth but is specialized in the complete reduction of the aboral tentacles, the partial reduction of the oral tentacles and in the reduction of the gonophores to cryptomedusoids (Text-fig. 52). The stem, too, is solid and highly muscular.

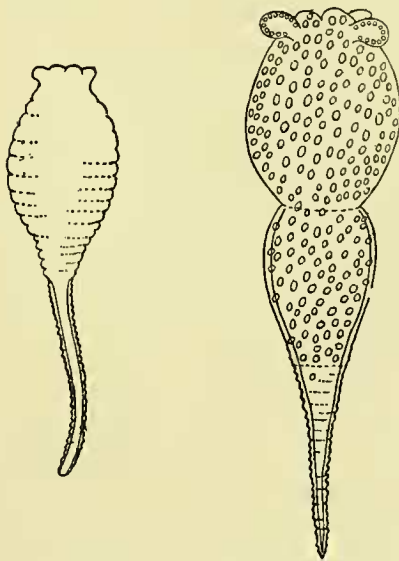


FIG. 52. *Boreohydra simplex* Westblad: a Corymorphine hydroid in which the aboral tentacles have been lost.

Corymorpha nutans M. Sars

Of the solitary hydroids this is one of the more highly evolved in the large size and elaboration of the individual polyp (Text-figs. 7 and 12). The medusa has evolved but little and is very similar to that in *Euphysa aurata* (a much simpler hydroid).

Features which may be regarded as related to size are: the large number of tentacles in the oral and aboral sets of tentacles, the parenchymatous cushion and diaphragm for the support of the aboral whorl of tentacles, proliferation of the budding area into long hollow branched blastostyles, parenchyma in the stem and the formation of stem canals, a large number of filaments and a more adherent perisarc resulting from a stiffening of the stem.

Apart from changes related to size this species is more advanced than *Euphysa aurata* in its filiform tentacles, but the larval hydroid still has capitate oral tentacles.

Tricyclusa singularis (Schulze)

This aberrant solitary hydroid is primitive in the possession of a gelatinous sheath-like stem perisarc, there appears to be no diaphragm and the oral tentacles are capitate (Text-fig. 6, p. 462).

This species has the above features in common with a possible *Euphysa*-like ancestor, but is specialized in the following characteristics: The interpolation of an additional whorl of tentacles, a reduced moniliform arrangement of nematocysts on the intermediate and aboral whorls of tentacles, a basal disk for attachment of the hydroid to the substratum and the reduction of the gonophores to cryptomedusoids.

Margelopsis haeckeli Hartlaub

Margelopsis haeckeli is one of the few pelagic species of Capitate hydroids (Text-fig. 31, p. 482). There is no stem, only an invagination with vacuolated cells. The hydranth conforms in external morphology to a Tubularian with two whorls of filiform tentacles in the adult.

The medusa has the ring gonad and simple mouth on the manubrium. The eggs develop into actinulae on the manubrium and this is considered a primitive feature found mainly in the Tubulariidae and only exceptionally in colonial corynids.

The medusae of *Margelopsis* and its near relatives are unique among Codonids in having several tentacles grouped together in each perradius, and this arrangement must be regarded as a specialized feature.

Pelagohydra mirabilis Dendy

Pelagohydra must be regarded as a highly modified Margelopsid (Text-fig. 21, p. 470). Its medusa however has remained essentially Margelopsid in character.

The *Pelagohydra* polyp is specialized in the following features: (1) The enormous development of the parenchyma of the diaphragm resulting in (2) The obliteration of the aboral chamber and much of the oral chamber with (3) The development of a peripheral canal system for feeding the tentacles and blastostyles and (4) The scattering of the aboral whorl of tentacles and also of the blastostyles.

Ectopleura dumortieri (van Beneden)

The *Ectopleura* hydroid, like *Tubularia*, has a firm adherent perisarc and the tentacles are all filiform in the adult; that is, it has progressed beyond the Corymorphine stages.

Its medusa has a much modified arrangement of the nematocysts on the tentacles, obviously derived however from the moniliform type, but in other respects, it is an ordinary Codonid medusa with ring gonad and simple mouth. In its possession of four perradial tentacles, and the exumbrellar nematocyst streaks, it is possibly more primitive than typical *Corymorpha* and *Euphysa* medusae (Text-fig. 41, p. 491).

Acaulis primarius Stimpson

Acaulis primarius retains the simple gelatinous tube and the filaments of the lower Corymorphine. It has, however, transformed its aboral whorl into thick, fleshy, filiform tentacles, and has developed scattered capitate tentacles in the intertentacular area (Text-fig. 13, p. 466). Its ancestor must have been an unspecialized Corymorphine which had lost the moniliform arrangement of the nematocysts but retained the gelatinous tube and the anchoring filaments. *Acaulis* has fixed gonophores.

Monocoryne gigantea (Bonnievie)

Monocoryne is a rather specialized species but it has retained a few stout anchoring filaments (Text-fig. 38, p. 488). Here the gelatinous tube has become a firm perisarc, the scattered capitate body tentacles of *Acaulis* have become fused in groups of three to form trifid (sometimes quadrifid) tentacles and the fixed gonophores are hermaphroditic.

Arum cocksii Vigurs

This Myriotheline hydroid (the *Myriothela phrygia* of Hincks) is possibly the most highly specialized solitary hydroid known (Text-fig. 15, p. 467). It has a simple lamellar perisarc at the base with modified anchoring filaments. In other respects, viz.: its numerous body tentacles, its branched coryniform blastostyles, its special claspers for the fertilized egg, the highly organized actinuloid larva and its ridged endoderm, it is highly specialized.

The related *Myriothela phrygia* (Fabricius) is notable for the absence of perisarc and for its retention of the anchoring filaments in a slightly modified form.

Asyncoryne ryniensis Warren

This is a colonial hydroid with a creeping stolon and a firm perisarc. In other respects the hydroid is rather primitive. Its hydranth suggests that it has evolved direct from the lower Corymorphines; it has an oral whorl of capitate tentacles and has retained the moniliform type of aboral tentacle. These, however, have become scattered over the body of the hydranth. Gonophores are fixed.

The structure of the hydranth, particularly the retention of the moniliform tentacle, indicates that this species has evolved along a different line from other corynoid hydroids (Text-fig. 3, p. 459).

Halocordyle tiarella (Ayres)

Halocordyle, better known as *Pennaria*, has an exceptionally well developed, upright, branched hydrocaulus with regular branching and possessing ringed perisarc at the origins of branches (Text-fig. 25, p. 474). As regards this feature it is more advanced than any member of the related family Corynidae.

Its hydranth is however little removed from the basic type of Corymorphine and its ancestor might well have been something rather like the larval *Corymorphantans*, the only essential difference in external morphology of the hydranth being the addition of scattered capitate tentacles between the oral capitate whorl and the aboral filiform whorl (Text-fig. 53). In the latter these aboral filiform tentacles are fully developed and are not reduced in any way.

The fully developed medusa is without tentacles and is seldom freed. Its structure is essentially Codonid.

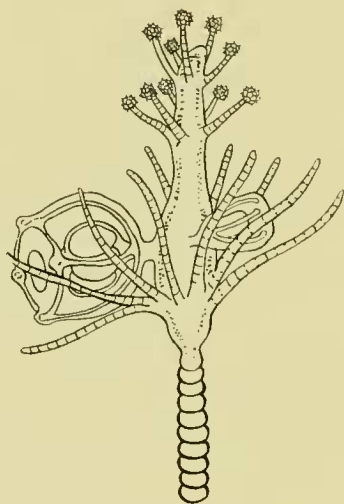


FIG. 53. *Halocordyle tiarella* (Ayres) with female medusa bud still attached (redrawn from Mayer, 1910).

Stauridiosarsia producta (Wright)

In this colonial Corynid there is a creeping stolon but the upright hydrocaulus is poorly developed. Here the hydranth has an oral whorl of capitate tentacles, scattered capitate body tentacles and a reduced whorl of aboral filiform tentacles (Text-fig. 10). These reduced filiform tentacles reflect the trend in the Corynidae where the filiform tentacles are lost (see p. 462).

The medusa has four radial canals, four perradial marginal tentacles, a ring gonad and simple mouth. All these are primitive features, and, together with the ocellus on each tentacle, are typical of Sarsiid medusae. The tentacles of this and other

species of corynid medusae reflect the varying degrees to which the ancestral moniliform condition of nematocyst armature has been reduced.

Cladocoryne floccosa Rotch

Cladocoryne is primitive in having an unbranched hydrocaulus and in the large size of its hydranth (Text-fig. 54). In other respects it is rather specialized, especially in its scattered coryniform tentacles. The origins of this form are obscure but it may have arisen from an unspecialized Acauloid stock where the tendency to develop coryniform tentacles may be noted in *Monocoryne* (where there are trifid capitate tentacles) and in the so-called blastostyles of *Arum cocksi*.

Cladocoryne has fixed gonophores borne on the body of the hydranth.

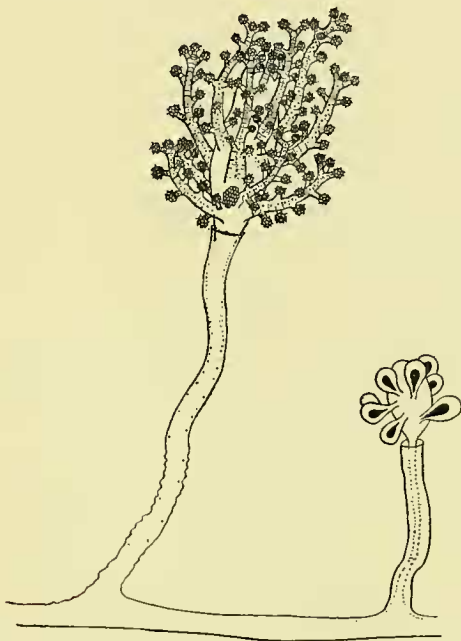


FIG. 54. *Cladocoryne floccosa* Rotch: two hydranths, one sterile and one reduced to a blastostyle (redrawn from du Plessis, 1881).

Cladonema radiatum Dujardin

The hydroid has a creeping stolon but an upright hydrocaulus is not developed. The hydranth retains all the essential features of a larval *Corymorpha*—an oral whorl of capitate tentacles and an aboral whorl of filiform ones. Medusa buds continue to be borne in the intertentacular area. All these are primitive characteristics.

The medusa retains certain primitive features, viz.: the Sarsiid ocellus and the continuous ring gonad. In other respects the medusa is highly specialized. There are 4-11 radial canals and a corresponding number of tentacles; the latter are coryniform with 1-4 stalked adhesive organs. The mouth has 4-5 lobes each armed with a nematocyst cluster.

This species is a good example of a very specialized medusa with a simple, little-changed hydroid (Plates 12 & 13).

Eleutheria dichotoma Quatrefages

In *Eleutheria dichotoma* (the hydroid was described by Hincks as *Clavatella prolifera*) the polyps arise from a creeping stolon; they are long and possess only an oral whorl of capitate tentacles, the aboral whorl being missing. In these characters the hydroid is simplified, but the medusa buds have moved down nearly to the base of the polyp away from the digestive area (Text-fig. 48, page 500).

The medusa is highly specialized and adapted to a creeping habit instead of a planktonic one. It has, however, retained the simple mouth and the Sarsiid ocellus. There are more than four radial canals and a corresponding number of tentacles; the latter are branched once and have an adhesive organ at the tip of one and a capitate head at the other. The gonads are in a special brood pouch situated above the stomach.

As in *Cladonema*, *Eleutheria* has a fairly simple hydroid and a much modified medusa.

Hydrocoryne miurensis Stechow

Hydrocoryne miurensis has the same simplified type of hydranth as *Eleutheria* but is rather specialized in the possession of a thickened gelatinous, ridged mesogloea in the hydranth and in the possession of an encrusting base with the same mesogloal thickening.

Its medusa has four radial canals, a ring gonad and four tentacles exhibiting traces of the moniliform arrangement of nematocysts. Here then the hydroid is much modified and the medusa retains the basic features of the Corynid medusa (Text-fig. 49, page 500).

Zanclea costata Gegenbaur

In this hydroid the polyps are typical Corynids without filiform tentacles (Text-fig. 47, page 499). The gonophores are borne on the hydranths and the latter may become reduced to complete blastostyles. There is however some indication that division of labour is setting in and that some polyps are less likely to bear gonophores than others.

The medusa retains the simple mouth, the four radial canals and the four tentacles of the Codonid. It has however many specialized features: the tentacles have numerous stalked abaxial capsules containing nematocysts, the exumbrellar nematocyst armature is confined to special tissue, the ocelli have been lost and the gonad is split up into four interradian groups.

Rosalinda williamsi Totton

As in *Zanclaea* the hydranth is typically corynid with numerous scattered capitate tentacles. The chief interest of the species lies in the fact that it has an encrusting base from which the hydranths arise. This encrusting base is believed to have an internal mesogloal skeleton as in the Solanderiidae.

The reproduction of this species is not known.

Dendrocoryne misakinensis Inaba

The simple Corynid hydranth is found here also but in other respects this species is one of the most advanced Capitate hydroids. There is an upright, branched gelatinous skeleton completely covered in ectoderm. The gonophores are not borne on the hydranths but on the rhizocaulome formation.

Ptilocodium repens Coward

This is an aberrant form found on the leaves of the pennatulid *Pennatula fimbriata* Herklots. The gonophores are borne at the base of the hydranth and are fixed eumedusoids with four radial canals and a ring gonad (Text-fig. 55).

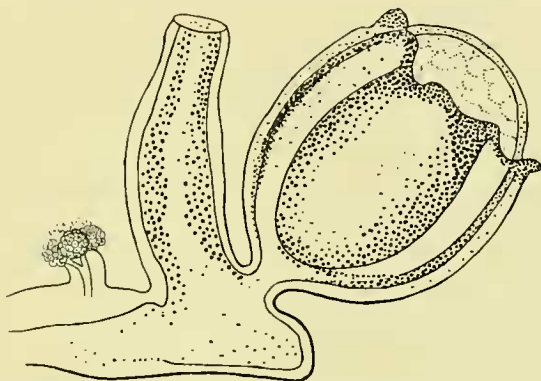


FIG. 55. *Ptilocodium repens* Coward, an aberrant Corynoid with a nutritive zooid and a dactylozooid (redrawn from Leloup, 1940).

The specialized features are many: the coenosarc is naked and encrusting, the sessile nutritive polyps have no tentacles, and there are sessile dactylozooids with four short capitate tentacles.

This species is insufficiently known but it may have a common origin with the ancestors of *Millepora*. Another interesting feature is the division of labour in the polyps, the one concerned with feeding and reproduction and the other with protection.

(b) Relationships

The division of the athecate hydroids into Capitata and Filifera by Kühn (1913) was a great advance on earlier classifications, and, if we omit species later removed

to the Limnomedusae, these two divisions (the one with capitate tentacles in the hydroid and a ring gonad in the medusa, and the other with filiform tentacles in the hydroid and a non-Codonid medusa) form natural groups which can be applied both to the hydroid and the medusa phases.

Kühn thought that the Corynidae were the most primitive Codonids and proceeded to derive the other families from them, and this is the scheme which has been in use ever since. Both Kramp (1949) and Russell (1953) have accepted the Corynidae as the most primitive family of capitate forms. Ample evidence has been brought forward here to demonstrate that on general principles the Corynidae as colonial animals are secondarily simplified, and I am in agreement with Totton (1954) that to derive solitary forms like *Tubularia* and *Corymorpha* from colonial ones is "most improbable".

The solitary forms are more primitive than the colonial forms for reasons already given and it is among these that we have to look for forms resembling the ancestral capitate hydroid. The lower Corymorphines *Euphysa* and *Hypolytus* retain many ancestral features and in all essentials could be the starting point for capitate evolution (Figs. 56-58).

From this type of hydroid may be traced three primary lines of evolution: (1) The *Tricyclusa* line represented by one species so aberrant that a new superfamily is justifiably created for it. (2) The *Asyncoryne* line represented by one species which has become colonial. (3) The higher forms including the colonial Capitata, the Tubularians and the *Acaulis-Myriothele* group (discussed further below).

The lower Corymorphines seem to have given rise to an unspecialized *Corymorpha* in which the oral capitate tentacles were retained and the aboral tentacles had become filiform. This must have been rather like the larval *Corymorpha nutans* and can be regarded as a basic type from which all other Capitate hydroids arose.

This basic type of hydroid appears to have evolved in three different ways to give rise to: (1) The *Corymorpha-Tubularia-Margelopsis* line, all essentially solitary forms; (2) The *Acaulis-Myriothele* line of solitary hydroids; (3) The colonial Corynoidea (except the Asyncorynidae and the Cladocorynidae).

These form three main groups which are raised to the rank of superfamilies in recognition of the separate, distinctive, evolutionary trends they display.

The *Tubularia* line, as the first may be called, arose from the lowly Corymorphine evolving filiform tentacles in the adult and a more or less complete diaphragm. From this the Tubulariidae may be assumed to have arisen through the evolution of a firm perisarc, loss of anchoring filaments with settlement of the larva on a firm substratum, together with partial atrophy of the diaphragm and the stem canals to form a sieve plate. *Branchiocerianthus*, too, as has already been explained, is unintelligible without a Corymorphine ancestry (p. 472).

The Margelopsidae, also, although aberrant pelagic forms, seem to have Tubularian affinities although the medusa has evolved along its own lines. In *Pelagohydra* as has been noted (p. 471) the diaphragm has become the float but not enough is known of the *Margelopsis* hydroid to estimate whether the diaphragm was present and has become reduced.

The *Acaulis*-*Myriothele* line stands on its own as a group of solitary hydroids. *Acaulis* is little removed from the basic type of Corymorphine with its gelatinous tube and filaments. This noticeable failure to develop a firm upright hydrocaulus and the tendency for the animals to become long and vermiform are characteristics of the group as a whole. Apart from the multiplication of capitate tentacles in the intertentacular area, there is a tendency towards the development of coryniform tentacles (trifid in *Monocoryne* and both simple and coryniform ones in *Arum cocksi* where the latter carry the gonophores).

The colonial Capitata classified here as the Corynoidea includes nearly all those species which I am inclined to think arose from a form like the larval *Corymorpha*, but two families, the Asyncorynidae and the Cladocorynidae (included in this superfamily because they are colonial forms) seem to have originated in a different way. The affinities of the former with the most primitive Corymorphines has already been noted but the Cladocorynidae may have arisen from early Acauloid stock where the tendency to produce a coryniform tentacle has already been indicated. Their position in this superfamily is, of course, tentative, but to include them in other or new superfamilies would not be justified at present for we do not know enough about the two species on which the families are founded. Picard (1955) places *Cladocoryne floccosa* Rotch in the Pteronematidae (Zancleidae of this report), but does not give sufficient reasons for the acceptance of his view here.

The morphology of the simpler Corynoid polyps is very little removed from the larval *Corymorpha* but they have become colonial with creeping stolons and rudimentary hydrocauli. Such polyps are found in *Cladonema*, *Dipurena* sp. (Vannucci 1956, in press) and in the larval *Stauridiosarsia*. The typical Corynids differ little from this basic type except in the disappearance of the filiform tentacles (persisting in some species as "false" tentacles) and the development of additional intertentacular capitate tentacles. The medusae differ but little from the basic type but each tentacle base has developed an ocellus. We see, too, the breaking up of the regular moniliform arrangement of the tentacular nematocysts.

The Halocordylidae seem to have branched off quite early from the Corynoid stem and have retained the filiform tentacles without reduction (as opposed to the Corynoid line where they have become progressively reduced and even lost) and have acquired additional intertentacular capitate tentacles on the hydranth. These together with an exceptionally well developed, branched hydrocaulus, are the chief features of Halocordylid evolution.

The Cladonemidae, the Eleutheriidae and the Hydrocorynidae seem to have arisen from the common Corynoid stock which also gave rise to the Corynidae and the Halocordylidae. The Hydrocorynidae soon evolved along a line whose chief characteristics were the loss of the filiform tentacles, the fusion of the basal stolons to form an encrusting base and the development of a thick gelatinous mesogloal skeleton. At the same time the medusa (when young at least) retained features which are essentially Sarsiid (Text-fig. 49, p. 500). In the Eleutheriidae, too, the filiform tentacles are lost (as in some Cladonemids) but the trophosome remains simple and it is the medusa which has evolved, as already noted, for a creeping mode

of life. In the Cladonemidae, also, the hydroid remains almost unchanged and in external morphology is still a simple Corynid of primitive appearance, but the highly evolved medusa has some features such as the adhesive organs and branching of the tentacles in common with that of *Eleutheria*. Although each family has been derived from a common stock they appear to have diverged early.

The Solanderiidae consist of both simple and branched forms, the one with an encrusting base and the other with an upright, branched formation. They are, as already indicated for *Dendrocoryne*, an advanced group with many specialized features but the form of the polyps (typical Corynids) suggests that they have arisen from the Corynid stock. The mesogloal skeleton may have arisen independently in this family and in the Hydrocorynidae, but this little known group should be studied in detail in places where living material is available.

The Ptilocodiidae also requires study. All that can be said is that it belongs to an aberrant Corynoid stock which probably also gave rise to the Milleporina, but it is itself too specialized to be regarded as an ancestral stage in their evolution (Text-fig. 55).

The Zancleidae of Russell is by definition (Russell, 1953, p. 98) an assemblage of forms in which the hydroids "have irregularly distributed tentacles, either all capitate, or all filiform or of both types" but all have zancleid medusae. It thus includes the Corynipteridae Weill and the Clavipteridae Weill (1934b). As Russell has mentioned only one species, *Zanclea costata*, this is the type of the family and fortunately it is well known. The mosaic presented by *Zanclea* implies that it arose from a Corynid stock by considerable evolution in the medusa. It has one type of nematocyst (macrobasal eurytele) which has not so far been reported in the lower Capitata.¹ This same type of nematocyst is also found in *Pteroclava* (a species with scattered filiform tentacles and a zancleid medusa), as well as in the Chondrophore *Verella* (Picard, 1955). The mosaic in *Pteroclava* is very similar to that in *Zanclea* and there is a suggestion here that the change from capitate to filiform tentacles is fairly recent in origin.

Picard (1955) has put forward a very interesting theory that the Chondrophora (*Verella*, *Porpita* and *Porpema*) have arisen from what he calls Pteronematidae, but before discussing this theory it may be desirable to ascertain what we mean by this name to-day.

This family, the Pteronemidae, was created by Haeckel (1879) as a subfamily of Cladonemidae and included the genera *Pteronema*, *Zanclea*, *Gemmaria* (synonymous with *Zanclea*) and *Eleutheria*. Subsequently Hartlaub (1907) transferred *Eleutheria* to the Dendronemidae (another subfamily of Cladonemidae) and added *Halocharis* and *Mnestra*, the one being, and the other probably, synonymous with *Zanclea*, to the Pteronemidae. Mayer (1910) referred *Zancleopsis* Hartlaub 1907 to the family.

Subsequently the families Eleutheriidae (Russell, 1953), and Zancleidae (Russell, 1953) were set up for their respective genera so that the Pteronemidae has become

¹ Undue significance should not be attached to the apparent absence of a macrobasal eurytele in the solitary Capitata for the nematocysts of these forms have been studied by very few workers. Sometimes a particular kind of nematocyst is found in the medusa and not the hydroid (and *vice versa*).

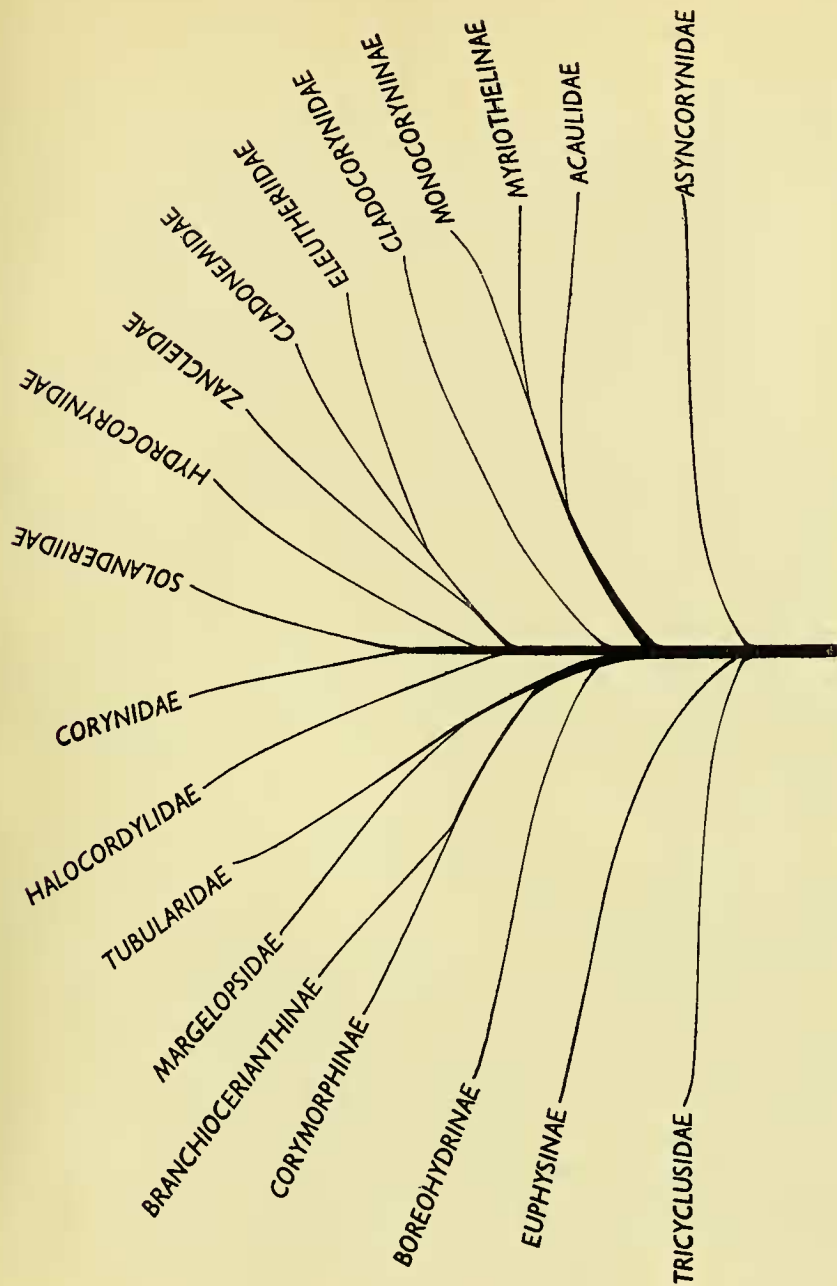


FIG. 56. Phylogeny in capitate hydroids: a diagram showing the relationships of the families of capitate hydroids.

restricted to *Pteronema* (itself an imperfectly understood genus) and *Zancleopsis* (which obviously does not belong to the family). Reference must also be made to the Cladonemidae, which has now been restricted to *Cladonema* and closely related forms by Russell (1953), and also to the Dendronemidae Haeckel, the second of Haeckel's Cladonemid subfamilies, containing the genera *Ctenaria*, *Cladonema* and *Dendronema*. The second of these genera, the type of the Cladonemidae, has been re-classified by Russell (1953) so that *Ctenaria* and *Dendronema* are excluded from the family. We are thus left with three genera, *Pteronema*, *Ctenaria* and *Dendronema* that are too imperfectly known to justify any re-definition of the family Pteronemidae.

In his theory that the Chondrophora are of "pteronemid" origin, Picard obviously uses the name in a general way, for he specifically mentions *Zanclea*, and makes some allusions to coryniform tentacles such as we find in the hydroid *Cladocoryne* and in the *Cladonema* medusa. As arguments in favour of this theory he points out that the macrobasic eurytele is common to *Zanclea* and *Veilella*, the exumbrellar nematocyst tracks are confined to special tissue both in the medusa of *Zanclea* and in the *Chrysomitra* medusa of *Veilella*, the resemblance of the gonozooid of *Veilella* to the fertile polyp in *Zanclea* and also points out the resemblances between the double perisarc of the *Zanclea* hydroid's hydrocaulus and the chitinized float of the Chondrophores. Picard is convinced that the Chondrophora has sufficiently strong "Pteronemid" affinities that he reduces them to the status of a family, the Chondrophoridae, to be placed next to his Pteronematidae.

I do not propose to discuss here whether the Chondrophora are evolved from pelagic tubularians, as Totton (1954) believes, or whether, as Picard suggests, that they are "pteronemid" in origin, but it is pertinent to this survey to mention that the differences which separate the Chondrophora from the Athecata (Anthomedusae) are as great as separate this group from the Thecata (Leptomedusae). For this reason, I believe the Chondrophora should have the status of an Order as maintained by Totton.

CLASSIFICATION

In the classification of the Capitata which follows, the hydroids and medusae are merged for the first time into a single coherent classification to replace the dual schemes that had prevailed so long.

The classification follows the broad evolutionary trends that have been traced in the earlier part of the report, and I think it is right that these lines should be grouped, as far as our knowledge goes, into superfamilies. I have hesitated to give superfamily rank to the Cladocorynidae and the Asyncorynidae because they are imperfectly known; they are thus placed in the Corynoidea simply because they are colonial and not because of any supposed common ancestry (but see pp. 514-515).

Nematocysts are of some use in denoting higher taxonomic groups and they are also of use in separating different species on size differences. They are however of little use at family level and in the Capitata so few forms have been studied that it is not wise to come to general conclusions. All that can be said is that the three main types seen are stenoteles, desmonemes and atriches in that order of frequency (Table IV). As so few forms have been studied, undue significance should not be

TABLE IV.

				Haplonemes.			Heteronemes.			
				Desmo- nemes.	Stenoteles.	Atrichous.	Basitrichous.	Anisotrichous.	Micro-basic mastigophores.	Macro-basic mastigophores. Euryteles. Euryteles.
Anthomedusae (<i>Atheata</i>)										
Corymorphidae										
<i>Corymorpha nutans</i> M. Sars	.	x		x		x	(x)	..
<i>Euphyssa aurata</i> Forbes	.	x		..		x	..	x
<i>Boreolhydra simplex</i> Westblad	.	x		x		x
Tubulariidae										
<i>Ectopleura dumortieri</i> (van Beneden)	.	x		x		x	x	..
Corynidae										
<i>Sarsia eximia</i> (Allmann)	.	x		x	
<i>Sarsia prolifera</i> Forbes	.	x		x	
<i>Sarsia gemmifera</i> Forbes	.	x		x	
<i>Syncorynide</i> C (Weill 1934b, p. 433)	.	x		..		x
Cladonemidae										
<i>Cladonema radiatum</i> Dujardin	.	x		x	
Eleutheriidae										
<i>Eleutheria dichotoma</i> Quatrefages	.	x		x	
Zancleidae										
<i>Zanclea costata</i> Gegenbaur	.	x		..		x
Chondrophora										
<i>Veletta veletta</i> L.	.	x		..		x	x
<i>Porpita mediterranea</i> Esch.	.	x		..		x	x

attached to the fact that both *Zanclaea* and *Velevella velevella* possess macrobasic euryteles.

Apart from the fact that this classification includes both hydroids and medusae, nearly all the medusa families defined by Russell (1953) are included without modification, for they form natural groups. The chief points of difference are the elevation of his Corymorphinae to the rank of a family (a step already taken by Kramp, 1949) and the creation of superfamilies.

As regards the earlier classifications of the hydroids, the classification now presented includes a re-distribution of many of the so-called Halocordylidae, the recognition of the Euphysinae, the creation of a sub-family for *Monocoryne gigantea*, a separate family, the Hydrocorynidae for *Hydrocoryne miurensis*, the creation of super-families, as well as bringing the hydroids into line with modern concepts in classifying their medusae.

Order ANTHOMEDUSAE (ATHECATA)

Hydroids with naked hydranths without distinct thecae. Reproductive polyps when present without gonothecae. Gonophores fixed or free medusae.

Newly liberated medusa deep bell-shaped, without statocysts and usually with swollen tentacle bases. Mature medusae with gonads always on stomach and occasionally extending for a short distance along the radial canals.

It is not possible to draw a sharp distinction between some Anthomedusan forms and those found in the Leptomedusae (Thecata) and in the Limnomedusae. There are some hydroids, particularly in the *Campanopsis* group of Haleciids, in which the hydranths are naked and there are many Leptomedusae and Limnomedusae in which there are no statocysts or other marginal sense organs in the medusa. The Limnomedusae in particular is a heterogeneous assemblage of forms some of which at least seem to have Codonid affinities, or, more precisely, a common ancestry with the Capitate hydroids.

Sub-order CAPITATA Kühn, 1913

Hydroids with some tentacles capitate either in the larva or in the adult. Gonophores usually borne on the body of the hydranth. Gonads in the medusa usually forming a continuous ring round the manubrium.

This is a very well defined group and the most primitive in the Anthomedusae although there are some solitary forms which have grown large and elaborate. In some Tubularian families capitate tentacles are found only in the very young hydroid, and in some aberrant medusae like *Zanclaea* and *Eleutheria* the gonads no longer form a continuous ring.

Super-family TUBULAROIDEA nov.

Hydroids usually solitary but some colonial forms occur. Hydranths with two sets of tentacles, capitate, filiform, or moniliform in type, but the aboral whorl is never capitate.

Medusae (when present) with or without exumbrellar nematocyst tracks, with stomachs not extending beyond bell margin, with simple circular mouths. Four radial canals with perradial tentacle bulbs without ocelli. Tentacles four or fewer, or grouped in perradial clusters.

This superfamily is essentially a group of solitary forms, although some species of *Tubularia* are colonial, but the colonial nature of several species of *Tubularia* is in doubt. There are many Tubularoids in which both sets of tentacles are filiform in the adult hydroid, but the oral tentacles of the very young hydroids are distinctly capitate. It includes the families Corymorphidae, the Tubularidae and the Margelopsidae. In the latter family the hydroids consist of pelagic hydranths modified for a planktonic existence; they are thought to provide a link with the Disconanth Siphonophora.

Family CORYMORPHIDAE Allman 1872.

Hydroids solitary, with perisarc feebly developed in the form of a gelatinous perisarcal sheath. Stem with anchoring filaments. Medusae, when present, with 1-4 perradial tentacles and without exumbrellar nematocyst tracks.

Type species: *Corymorpha nutans* M. Sars, 1835.

There are four sub-families, the Euphysinae, the Corymorphinae, the Boreohydrinae and the Branchiocerianthinae. The Euphysinae (suggested by Haeckel, 1879, for *Euphysa* medusae) is re-established now, to mark the wide gulf which exists between the hydroids of the lower Corymorphines (*Euphysa*, *Hypolytus* and possibly *Gymnogonos*) and the elaborate higher Corymorphines like *Corymorpha*, which have filiform tentacles, stem canals and an exceptionally well-developed diaphragm. *Branchiocerianthus* can be regarded as essentially a Corymorphine, despite its secondarily acquired bilateral symmetry, and is accordingly given the rank of a sub-family.

Sub-family EUPHYSINAE

Hydranths radially symmetrical, without diaphragm and without fully developed stem canals. Oral tentacles, capitate or moniliform, aboral tentacles moniliform. Fixed gonophores or free medusae.

Type species: *Euphysa aurata* Forbes.

Sub-family CORYMORPHINAE

Hydranths radially symmetrical, with diaphragm, and stem canals. Tentacles all filiform in the adult hydroid. Fixed gonophores or free medusae.

Sub-family BOREOHYDRINAE

Hydranths radially symmetrical, without diaphragm, with one whorl of oral capitate tentacles. Aboral whorl missing. Fixed gonophores, where known.

Type species: *Boreohydra simplex* Westblad, 1937.

There appears to be no justification for keeping *Boreohydra* in a separate family of its own as proposed by Westblad, and I propose to treat it as an aberrant Corymorphine.

Sub-family BRANCHIOCERIANTHINAE

Hydranths bilaterally symmetrical, with diaphragm, with two sets of filiform tentacles.

Fixed gonophores (where known).

Type species: *Branchiocerianthus urceolus* Mark, 1898 (Text-figs. 23-24, pp. 472-473).

Family TUBULARIIDAE Allman, 1864

Hydroids essentially solitary but with some colonial forms. Stems covered with firm perisarc. Hydranths with two whorls of filiform tentacles in the adult. Anchoring filaments very seldom present.

Gonophores fixed or free medusae. Medusae (when present) usually with per-radial exumbrellar nematocyst tracks.

Type species: *Tubularia indivisa* Linnaeus, 1758 (Text-figs. 17, 20 & 22, pp. 468, 470 & 471).

Family MARGELOPSIDAE Uchida, 1927

Pelagic hydranths with filiform tentacles in the adult. There is an oral whorl of tentacles but the aboral one may be scattered.

Medusae with perradial groups of tentacles at bell margin or at different levels on exumbrella.

Type species: *Margelopsis haeckeli* Hartlaub, 1897 (Text-fig. 31, p. 482).

Sub-family MARGELOPSINAE Rees, 1941

Margelopsidae without a distinct float and with an aboral whorl of tentacles.

Sub-family PELAGOHYDRINAE

Margelopsidae in which the posterior half of the hydranth is modified to form a float. Aboral tentacles scattered.

Type species: *Pelagohydra mirabilis* Dendy, 1902 (Text-fig. 21, p. 470).

Super-family TRICYCLUSOIDEA nov.

Hydroids solitary with three whorls of tentacles.

This super family is created for *Tricyclusa singularis* which is a rather unique kind of hydroid which does not fit in with the *Corymorpha-Tubularia* group or with the *Acaulis-Myriothele* group, but all three groups may be said to have originated from a primitive Corymorphine stock.

Family TRICYCLUSIDAE Kramp, 1949.

Hydroids solitary with a basal anchoring disk and gelatinous sheath-like perisarc. Hydranth with an oral whorl of capitate tentacles and two aboral whorls of imperfect moniliform tentacles.

Gonophores, fixed (where known)

Type species: *Tricyclusa singularis* (Schulze, 1876) (Text-figs. 6 & 51B, pp. 462 & 505).

Super-family ACAULOIDEA nov.

Hydroids solitary, with numerous scattered capitate tentacles, and sometimes other kinds of tentacle. Perisarc either feebly developed, as a gelatinous sheath or as a chitinized tube or almost absent. Anchoring filaments are present. Gonophores, fixed (where known).

This new superfamily includes the Acaulidae and the Myriothelidae.

Family ACAULIDAE Fraser, 1924

Hydroid with gelatinous tube and anchoring filaments. Numerous capitate tentacles scattered distal to the aboral whorl of large fleshy filiform tentacles; the latter may be absent in some species.

Gonophores, fixed (where known).

Type species: *Acaulis primarius* Stimpson, 1854 (Text-fig. 13, p. 466).

Family MYRIOTHELIDAE Hincks, 1868

Hydroid with or without chitinized perisarc tube, anchored by filaments. Numerous simple or compound tentacles with or without coryniform branched tentacles which may act as blastostyles.

Gonophores fixed (where known).

Type species: *Myriothela phrygia* (Fabricius) (Text-fig. 36, p. 487).

Subfamily MONOCORYNINAE Rees, 1956¹

Myriothelid polyp with basal perisarc tube and a few stout anchoring filaments. Trifid capitate body tentacles. Gonophores borne in the axils of the tentacles all over the body of the polyp.

Each gonophore is hermaphroditic.

Type species: *Coryne gigantea* Bonnevie, 1898 (Text-fig. 38, p. 488).

The sole genus is *Monocoryne* Broch, 1909, with one species known only from Hammerfest and Trondheim, Norway.

Subfamily MYRIOTHELINAE nov.

Myriothelid polyp, with or without basal perisarc sheath with simple or modified

¹ In press (*Nyt Mag. Zool. Oslo*).

anchoring filaments. Simple capitate body tentacles. Gonophores sometimes borne on special coryniform branched tentacles.

Super-family Corynoidea nov.

Colonial hydroids with either a firm closely adherent perisarc, an encrusting base, or an upright rhizocaulome formation. Hydranths simple, without diaphragm and with an oral whorl of capitate tentacles.

Medusae (where present) with or without exumbrellar nematocyst tracks, with stomachs sometimes extending beyond bell margin, with simple circular mouths or with short lips armed with nematocyst clusters. Four or more radial canals with corresponding number of tentacle bulbs, with or without ocelli. Tentacles simple, bifurcating, or branched. Gonophores fixed or free medusae.

Family ASYNCORYNIDAE Kramp, 1949.

Hydranths arising from a creeping stolon. Hydranth with an oral whorl of capitate tentacles and scattered moniliform tentacles.

Gonophores fixed (where known).

Type species: *Asyncoryne rnyiensis* Warren, 1908 (Text-fig. 3, p. 459).

Asyncoryne is the sole genus known and appears to have arisen independently from a primitive Corymorphine stock and has retained the moniliform tentacles.

Family CLADOCORYNIDAE Allman 1872

Hydranths borne on long perisarc-covered stems arising from creeping stolons. Oral whorl of tentacles capitate, the remainder coryniform.

Gonophores fixed (where known).

Type species: *Cladocoryne floccosa* Rotch, 1871 (Text-fig. 54, p. 511).

Family HALOCORDYLIDAE Stechow, 1923

Branched upright colonies with firm tubular perisarc. Hydranths with an oral whorl of capitate tentacles, an aboral whorl of fully developed filiform tentacles, with, in addition, scattered capitate tentacles between the two whorls.

Gonophores eumedusoid (where known).

Type species: *Halocordyle tiarella* (Ayres) (Text-fig. 25 & 53, pp. 474 & 510).

Family CORYNIDAE Johnston, 1836.

Corynoidea with upright stems, with firm perisarc, arising from creeping stolons. Hydranths, with oral capitate whorl of tentacles, usually with scattered capitate tentacles on body of hydranth, and with or without a vestigial whorl of filiform tentacles.

Fixed gonophores or free medusae. Medusae without exumbrellar nematocyst

tracks, with four radial canals, four perradial tentacle bulbs with ocelli and four tentacles. Stomach with simple circular mouth.

Type species: *Coryne pusilla* Gaertner.

Family CLADONEMIDAE Allman, 1872.

Corynoidea with short stems with firm perisarc arising from creeping stolons. Hydranths with oral whorl of capitate tentacles and usually an aboral whorl of reduced filiform tentacles; without diaphragm.

Medusae with manubrium with short mouth lips armed with nematocyst clusters, with variable number of radial canals, simple or branched, and with corresponding number of tentacles. Tentacle bulbs with ocelli. Tentacles branched and with organs of adhesion.

Type species: *Cladonema radiatum* Dujardin (Pl. 12 & 13).

Family ELEUTHERIIDAE Russell, 1953.

Corynoid hydroids, with an oral whorl of capitate tentacles, with or without aboral whorl of reduced filiform tentacles.

Creeping medusae with thickened ring of nematocysts round umbrella margin. Simple circular mouth, without special armature. Radial canals variable in number, simple or branched, corresponding to number of tentacles; the latter have ocelli, organs of adhesion and may be branched. Gonads in a special brood pouch above the stomach.

Type species: *Eleutheria dichotoma* Quatrefages, 1843 (Text-fig. 48, p. 500).

Family HYDROCORYNIDAE nov.

Corynoidea with thick encrusting base. Hydranths columnar, with only an oral whorl of capitate tentacles around a conical hypostome, and with thick chitinous mesogloea.

Gonophores borne in clusters near the base of the hydranth. Newly liberated medusa (where known) with deep bell shape, four radial canals and four tentacles each with swollen bulb and ocellus. Stomach short with simple circular mouth.

Type species: *Hydrocoryne miurensis* Stechow, 1907 (Text-fig. 49, page 500).

Family PTILOCODIIDAE Coward, 1909.

Corynoidea with naked anastomosing stolons forming a continuous coenosarc. Nutritive polyps without tentacles, dactylozooids with one whorl of capitate tentacles.

Gonophores fixed (where known) borne at the base of the nutritive zooid.

Type species: *Ptilocodium repens* Coward, 1909 (Text-fig. 55, page 513).

Family SOLANDERIIDAE Marshall, 1892.

Corynoid colonies with mesogloal skeleton, either in the form of an encrusting base, or as anastomosing branches, completely enclosed in ectoderm. Hydranths with scattered capitate tentacles.

Gonophores fixed (where known) arising directly from the coenosarc and not from the body of the hydranth.

Type species: *Solanderia gracilis* Duchassaing & Michelin.

Family ZANCLEIDAE Russell, 1953.

Hydroids with irregularly distributed tentacles, either all capitate, or all filiform, or of both types.

Anthomedusae with, or without, exumbrella nematocysts confined to specialized tissue in the form of oval or club-shaped patches or elongated tracks, with simple circular mouth; with four radial canals; with inter-radial gonads; with two or four hollow marginal tentacles, each with abaxial stalked capsules (or cnidophores) containing nematocysts, or without marginal tentacles; without ocelli.

Type species: *Zanclea costata* Gegenbaur (Text-fig. 47, p. 499).

The above definition was given by Russell (1953). In *Pteroclava* the filiform tentacles are actually slightly club-shaped and it appears likely that they are capitate when young. Consequently they have not been mentioned in the definition of the super-family (see p. 516 for a discussion of the family's status).

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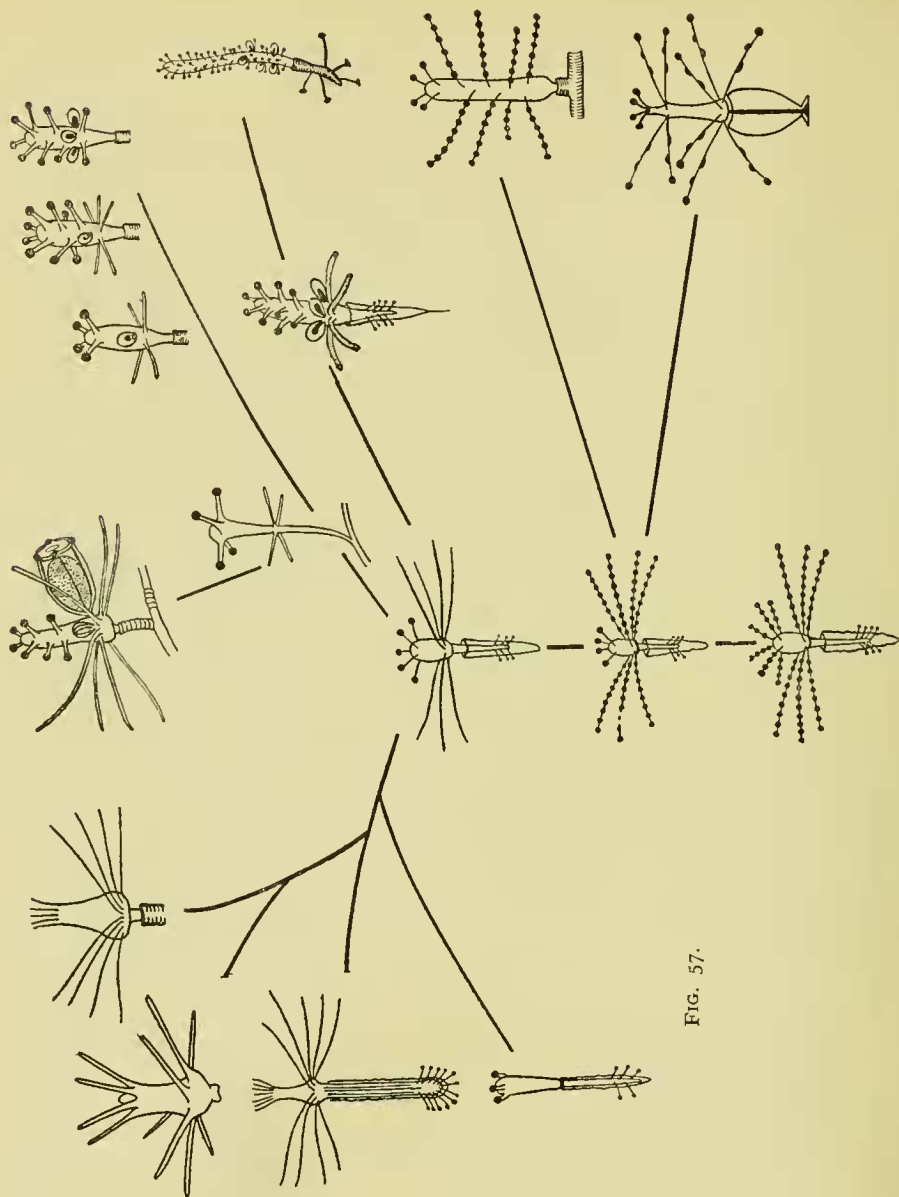


FIG. 57.

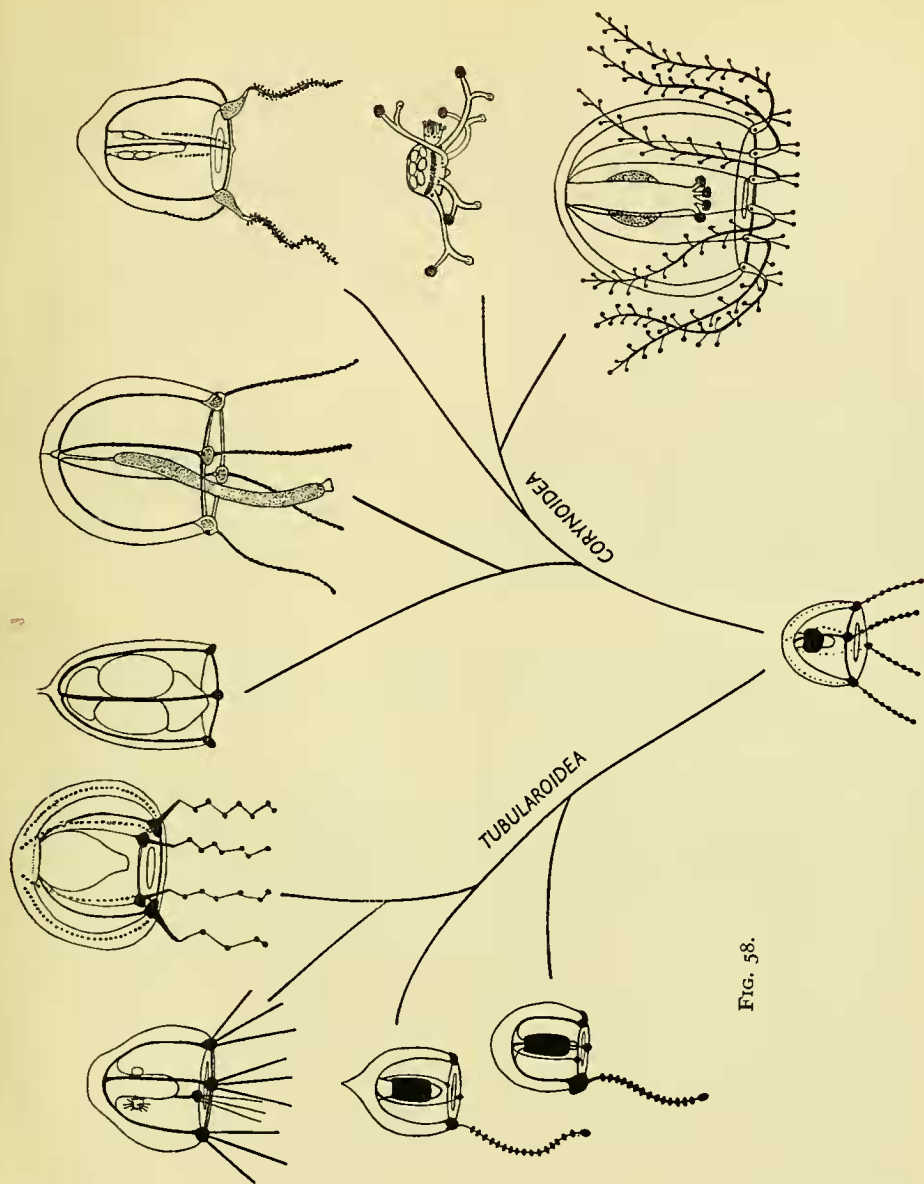


FIG. 58.

EXPLANATION OF FIGURES AND PLATES

FIG. 57. A diagrammatic representation of the main evolutionary trends in capitate hydroids in which the different hydroid types are represented by stylized sketches representing groups rather than individual species.

FIG. 58. Relationships of the different codonoid medusae; it will be noted that some aberrant Corynoid medusae have been included and that no medusae are known in the Tricyclusoidea and the Acauloidea.

PLATES 12 AND 13

Cladonema radiatum Dujardin

Photographs of living polyps and medusae taken by the shadowgraph method by the late Mr. O. E. Challis from colonies maintained in aquaria by Mr. F. J. Lambert, Leigh-on-Sea, Essex.

PLATE 12

FIG. 1. Typical sterile polyp with four oral capitate tentacles and four filiform aboral tentacles.

FIG. 2. Another polyp with six oral tentacles and a young medusa bud.

FIG. 3. The same hydranth as in Figure 2 with the medusa nearly ready for liberation.

FIG. 4. Another hydranth reduced to a blastostyle with one fully developed medusa.

PLATE 13

Cladonema radiatum Dujardin

FIG. 5 and 6. Different views of the medusa, seen in Plate 1, fig. 4, prior to liberation. Note that the blastostyle is completely reduced.

FIG. 7 and 8. Two views of the sexually mature medusa.



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